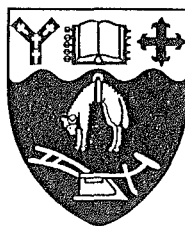


ECOLOGY AND BIOLOGY OF THE BANDED WRASSE,
NOTOLABRUS FUCICOLA (PISCES:LABRIDAE) AROUND
KAIKOURA, NEW ZEALAND.

A thesis submitted in the partial fulfillment
of the requirements for the Degree of
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Notolabrus fucicola, a large common labrid inhabiting shallow waters around New Zealand and Southern Australia, were collected monthly (Dec 1996 to Feb 1998) around Kaikoura. They were found to be pelagic synchronous spawners and followed the typical labrid spring-summer seasonal pattern of reproduction (July to December). Compared to other New Zealand labrids that are protogynous hermaphrodites, *N. fucicola* was found to be a secondary gonochorist, where individuals change sex before maturation. Although two colour phases are present, they are a monochromatic species with males and females found in all size classes and colour phases (a ratio of females to males 1.6: 1). Sexual maturity is attained between 2 - 3 years old and they can live upwards of 25 years. There was no significant difference in numbers across time or depth for *N. fucicola* but a significant difference was recorded for size with depth. *N. fucicola* is a generalist predator with seasonal variations in prey items. There were size specific changes in the diet from soft to hard-bodied prey. Seasonal variations were also recorded in gut fullness and condition. They are a territorial species that are likely to defend areas for food or shelter, but not spawning.

CHAPTER ONE

GENERAL INTRODUCTION

1.1 GENERAL INTRODUCTION

The Labridae, a family of marine fishes found primarily in tropical and temperate waters, number between 500 and 600 species and are one of the most abundant and diversified of all fish families in shape, colour and size (Nelson, 1984; Wainwright, 1991; Helfman *et al.*, 1997). Labrids (wrasses) are conspicuous members of fish assemblages on tropical and temperate reefs in different parts of the world and constitute a characteristic element of shallow water faunas. Due to their abundance on tropical reefs, the biology and ecology of tropical labrids have been studied extensively. However, there has been little investigation on the biology and ecology of the twenty-one labrid species found in New Zealand, with the exception of the spotty, *Notolabrus celidotus* (Jones, 1980, 1981a, b, 1984a, b, c).

The general biology and ecology of the ubiquitous banded wrasse, *Notolabrus fucicola*, is poorly known (Paulin and Roberts, 1992) with most information obtained from brief outlines in fish identification books (Graham, 1956; Roughly, 1961; Doak, 1978; Thompson, 1981; Last *et al.*, 1983; Nelson, 1984; Paul, 1986; Francis, 1988; Ayling & Cox, 1987; Paulin & Roberts, 1992; Kuitert, 1993; Paul and Moreland, 1993; Edgar, 1997). On average, *N. fucicola* are 20 to 30 cm in length, but can grow up to 60 cm and weigh as much as 5 kg (Paul, 1986, Ayling & Cox, 1987). *N. fucicola* have a widespread distribution throughout the nearshore waters of New Zealand, the Chatham Islands, Tasmania and southern Australia (Ayling & Cox, 1987; Paulin & Roberts, 1992; Kuitert, 1993; Paul & Moreland, 1993; Lincoln-Smith & Jones, 1995). The two studies that have gone into any depth on this species have been theses (Choat, 1962; Barrett, 1995a). Choat (1962) provided a detailed description of the morphology of *N. fucicola*, as well as briefly describing their habitat, diet, and nocturnal behaviour. Barrett (1995a) examined the movement, growth rates and reproductive biology of *N. fucicola*.

Overall, research on New Zealand reef fishes has been limited (reviews in Choat, 1982; Jones, 1988). The majority of ecological studies on New Zealand fishes have been limited to the warmer waters of northeastern New Zealand (Russell, 1971; Jones, 1980, 1981a, b, 1984a, b, c; Jones & Thompson, 1980; Leum & Choat, 1980; Ayling, 1981; Choat & Kingett, 1982; Choat & Ayling, 1987; McCormick & Choat, 1987; Choat *et al.*, 1988; Connell & Jones, 1991). These studies have been primarily concerned with relationships between habitats and fish associations and the feeding effects on benthic assemblages (Jones, 1988; Russell, 1988). However, little work has been done ^oin reef fishes along the east coast of the South Island, with the exception of Hickford (1993) and Hickford & Schiel (1995).

Temperate rocky reef environments support a wide variety of fish species that are dependent on the reef substratum, macroalgae and associated invertebrates for food and shelter. The physical and biological characteristics of a reef habitat, such as topographic complexity, substrate type, and algal cover appear to have a major influence on the distribution and abundance of reef fishes (Russell, 1977; Willan *et al.*, 1979; Kingett & Choat, 1981; Jones, 1984a, b, c; Choat & Ayling, 1987; Levin, 1993; Carr, 1994). Temperate reefs in New Zealand are characterised by macroalgae that can exhibit substantial variation both spatially and temporally (Choat & Schiel, 1982; Schiel and Foster, 1986). This variation can strongly influence the species abundance and composition of reef fish (Hobson, 1972; Ogden & Ehrlich, 1977; Jones, 1984c; Larson & DeMartini, 1984; Carr, 1989, 1991; DeMartini & Roberts, 1990). Macroalgae are important sources of food (Jones, 1984b; Schmitt & Holbrook, 1986; Carr, 1991), shelter (Ebeling & Laur, 1985; Behrems, 1987; Choat & Ayling, 1987; Anderson, 1994), recruitment habitats (Jones, 1980; Choat, 1982; Holbrook & Schmitt, 1988) and spawning sites (Jones, 1984a; Choat & Ayling, 1987; Holbrook *et al.*, 1994).

Nearshore habitats in Southern New Zealand differ biologically and physically from those in the North Island. The dominant algae differs between northern and southern New Zealand. The stipitate kelp *Ecklonia radiata* dominates in the

north, while in the south, the fucalean algae *Marginariella boryana* is the dominant ^{algal} kelp species in the shallow subtidal zone (Choat & Schiel, 1982; Schiel & Foster, 1986). One major habitat missing in most of southern New Zealand is the large echinoid-dominated areas common in northeastern New Zealand (Schiel, 1990). Furthermore, reefs around Kaikoura generally have steeper topography than the gradually sloping reefs of many northern New Zealand areas.

Fish numbers have been found to vary significantly over a wide range of temporal and spatial scales in tropical (Choat & Bellwood, 1985), subtropical waters (Schiel *et al.*, 1986), temperate (Russell, 1977; Leum & Choat, 1980; Kingett & Choat, 1981; Choat *et al.*, 1988; Holbrook *et al.*, 1994), and subantarctic waters (Kingsford *et al.*, 1989). Temporal variability appears to depend on the species or populations concerned, but the general consensus is that the composition and abundance of fish assemblages is fairly constant over time (years) (Ebeling *et al.*, 1980; Kingett & Choat, 1981; Stephens & Zerba, 1981; Jones, 1984c; DeMartini & Roberts, 1990; Holbrook *et al.*, 1994).

The trend for increasing size with depth appears to be a common feature of many fish species (Olla *et al.*, 1974; Johannes, 1978; Jones, 1981; 1984c; Choat & Ayling, 1987; Kingsford *et al.*, 1989; McCormick, 1989a; Green, 1996; Gillanders, 1997). Many labrids undergo size-specific changes in foraging habits and diet, for example, from algal to rocky substrata (Jones, 1980, 1984b; Kingett & Choat, 1981; Russell, 1983; McCormick, 1995a; Gillanders, 1997).

The diet and feeding behaviour of several New Zealand temperate reef fish have been investigated, mainly around northeastern New Zealand (see Jones, 1988). As with most labrids, *N. fucicola* are generalist predators and highly opportunistic feeders with a preference for crabs, gastropods and molluscs and amphipods (Choat, 1962; Doak 1972; Russell, 1973, 1983; Ayling & Cox 1987; Paulin & Roberts, 1992). Most generalist benthic carnivores exhibit seasonal variations in diet and feeding rate. This variation may be due to changes in abundance and activity of prey populations, fluctuations in water temperature,

and reproductive activity (Choat, 1982; Jones, 1988). The effect fish have on the invertebrate fauna of temperate reef fish population is uncertain. Some authors regard fish as having an important role in the subtidal zone (Ayling, 1981; Russell, 1983; Hixon, 1986; McCormick, 1995; Helfman *et al.*, 1997), whereas others conclude that reef fish are unlikely candidates for maintaining the structure of invertebrate communities (Choat & Kingett, 1982; Choat & Ayling, 1987). This debate will be discussed later.

Most labrids are protogynous hermaphrodites changing from a functional female to a functional male (Warner, 1975a). The reproductive patterns of many labrids, particularly tropical species, have received extensive treatment (Robertson, 1972; Roede, 1972; Robertson & Choat, 1974; Warner, 1975a, 1984; Robertson & Warner, 1978; Warner & Robertson, 1978; Tribble, 1982; Warner & Lejeune, 1985). However, only a few authors have investigated the reproductive biology of temperate labrids (Dipper & Pullin, 1979; Jones, 1980, 1981a, b; Gillanders, 1995a, b, 1997; Barrett, 1995a). In the Southern Hemisphere, the majority of temperate labrids investigated so far have been protogynous hermaphrodites (see Thompson, 1981; Barrett, 1995a). This is in contrast to several Northern hemisphere species that are reported not to change sex, such as *Centrolabrus exoletus*, *Crenilabrus melops*, *Ctenolabrus rupestris* (Dipper & Pullin, 1979; Warner & Lejeune, 1985) and several *Symphodus* species (Bentivegna & Beneditto, 1989). There is confusion in the literature about the reproductive pattern of *Notolabrus fucicola*. Many authors have reported this species to be a protogynous hermaphrodite (Doak, 1972; Thompson, 1981; Ayling & Cox, 1987; Francis, 1988). However, Barrett (1995a) and Jones (pers. com.), the only workers to examine the reproductive biology of *N. fucicola*, reported this species were secondary gonochorists. Secondary gonochorism occurs when all fish initially develop as females with some changing sex to males before maturation. Therefore, they are not hermaphrodites as they function only as a male or a female, ^{but} not both.

Spawning of most inshore temperate species is restricted to spring and summer (Jones, 1988; Kingsford, 1988; Ebeling & Hixon, 1991; Helfman *et al.*, 1997)

and appears to be influenced by water temperature (Robertson, 1980). The spawning season of *N. fucicola* has been reported to be approximately five months long, occurring from July until December (Doak, 1972; Jones, 1980, 1984b; Jones & Thompson, 1980; Robertson, 1980; Barrett, 1995a). Like most nearshore marine fishes, *N. fucicola*, has planktonic eggs and larvae (Robertson, 1973, 1980; Russell, 1988). Labrids generally recruit during the summer months and are normally found on shallow rocky substrates with high algal cover (Roede, 1972; Levin, 1993; Carr, 1994; Garcia & MacPherson, 1995).

Labrids are characterised by the great variation of colour and patterns they display during their growth (Roughley, 1961; Roede, 1972; Warner & Robertson, 1978; Paulin & Roberts, 1992). Two colour phases are recognised in labrids, the initial and terminal phase (Warner & Robertson, 1978; Wainwright, 1991). Generally, females predominate in the smaller initial phase (IP) and males occur almost exclusively in the terminal phase (TP). The initial phase colouration of *N. fucicola* can vary greatly, but tends to be red-brown to mottled olive green with a series of yellow dots over the body (Plate 1.1). The basic terminal phase colouration is dark purple-blue with six distinct yellow bands on the body and fins (Plate 1.2) (Choat, 1962, 1968; Doak, 1972, 1978; Last *et al.*, 1983; Paul, 1986; Ayling & Cox 1987; Francis, 1988; Kuiter, 1993; Paulin and Roberts, 1993). These yellow bands were often indistinct in a number of adult specimens (Choat, 1968). Colour change to the terminal phase occurs at around 250 mm long, but can occur over a broad size range of 150-300 mm in length (Doak, 1978; Thompson, 1981). The transitional individuals exhibit characteristics of both colour phases and the change to terminal phase colouration may take over two months. This change is permanent and individuals cannot revert back to initial phase colouration (Warner & Robertson, 1978). Some authors describe the sexes as dichromatic, that is, males and females have distinct colouration, (Doak, 1972; Francis, 1988) and others claiming the sexes are monochromatic, ^{having} no demarcation of colour with sex (Choat, 1962; Russell, 1988; Kuiter, 1993; Edgar, 1997).

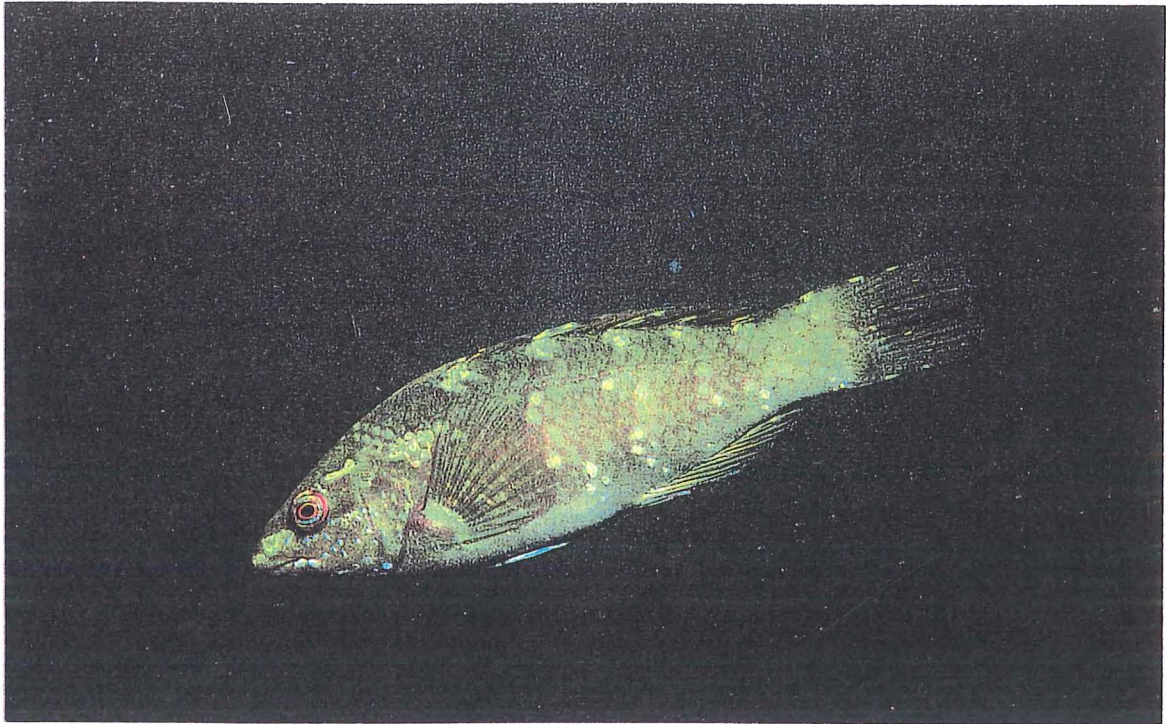


Plate 1.1 Photo of an initial phase *Notolabrus fucicola* (reproduced from Francis, 1988).



Plate 1.2 Photo of a terminal phase *Notolabrus fucicola* (reproduced from Francis, 1988).

Because *Notolabrus fucicola* exhibits varying degrees of dichromatism it was described by taxonomists as two distinct species, *Pseudolabrus pittensis* and *P. fucicola*. Choat (1968) concluded that the differences in colour pattern used to distinguish *P. fucicola* and *P. pittensis* was merely due to methods of preservation and the name *P. fucicola* had priority. This species, previously in the genus *Pseudolabrus*, has only been recently placed in the genus *Notolabrus* by Russell (1988). *Notolabrus* is from a combination of the Greek *notos*, south, and *labros*, wrasse, meaning "southern wrasse" in reference to the southern distribution of this genus (Russell, 1988); *fucicola* is a combination of the Latin *fucus*, a seaweed, and *cola*, dweller, in reference to the seaweed dwelling habits of this fish (Russell, 1988; Paulin & Roberts 1992). *Notolabrus fucicola* has been referred to as Banded Parrotfish (Doak 1972), Blue Wrasse, Purple Wrasse, Southern Wrasse, Winter Bream, Yellow-saddled Wrasse, Purple Parrotfish (Last *et al.* 1983), Chinaman (Thompson, 1981), Kelpie, Kelpfish, Butterfish (Paul & Moreland, 1993) and Taangahangaha (Francis, 1988).

Little is known about the growth, age and size at maturity for *N. fucicola*. Paul (1992), in a review of aging studies in New Zealand, found only a brief mention of measured growth of *N. fucicola* at the Portobello Marine Hatchery (Thomson & Anderton, 1921) but did not mention their results. Francis (1988) noted that *N. fucicola* can initially grow rapidly, reaching 120 mm at the end of their first year, and maturing during their second year at 180 mm. Conversely, Ayling & Cox (1987) reported they are relatively slow growing but did not mention growth rates. The maximum age of *N. fucicola* has been estimated to range from 17 years (Barrett, 1995a) to 25 years (Ayling & Cox, 1987). Presently, work on *N. fucicola* is being carried out in Australia on the size and age structure of the population, growth rates, and age at reproductive maturity. This is primarily due to the lucrative live fishery involving *N. tetricus* and *Notolabrus fucicola* (Anon, 1997).

Few behavioural studies have been done on marine fishes in habitats other than coral reefs (Grant, 1997). Many species of labrids display territorial behaviour and this is usually due to defence of spawning sites. Interspecific aggression is unusual but does occur between *N. fucicola* and other species (Ayling, 1980). Wrasses are predominantly diurnal and inactive at night.

This thesis ^{is} investigating habitat associations, reproductive and feeding ecology, and behaviour of *Notolabrus fucicola*.

1.2 STUDY AREA

The Kaikoura Peninsula is located between latitudes 42° 25' 11" and 42° 23' 22" south and longitudes 173° 39' 00" and 173° 44' 00" east on the northeastern coastline of the South Island of New Zealand. It projects approximately 4 km out to the sea from the Marlborough coastline (Davison & Van Berkel, 1985) (Figure 1.1). The Kaikoura region is unique in its geography in that the continental shelf drops sharply from 100 to 1500 metres to the continental slope. This shelf rises up from the southern extremity of the Hikurangi Trough off the Kermadec Trench to reach a depth of 2300 m approximately 20 km southeast of the Peninsula (Rasmussen, 1965). Between Hamuri Bluffs and South Bay the edge of the continental shelf is never more than 2 km offshore. Because of these trenches, upwelling currents along the coast bring nutrient-rich deep water to the surface, supporting phytoplankton blooms nourishing the zooplankton on which many fish feed (Bone *et al.*, 1995).

Kaikoura is centered on the subtropical convergence of the north-flowing cold subantarctic Southland (or Canterbury) Current and the warm water southerly flowing East Cape Current (Heath, 1972). The relative importance of these currents varies seasonally. For example, the Southland Current exerts its greatest influence on the region during the winter months, when as increased frequency and strength of winds from the south increases the onshore transport

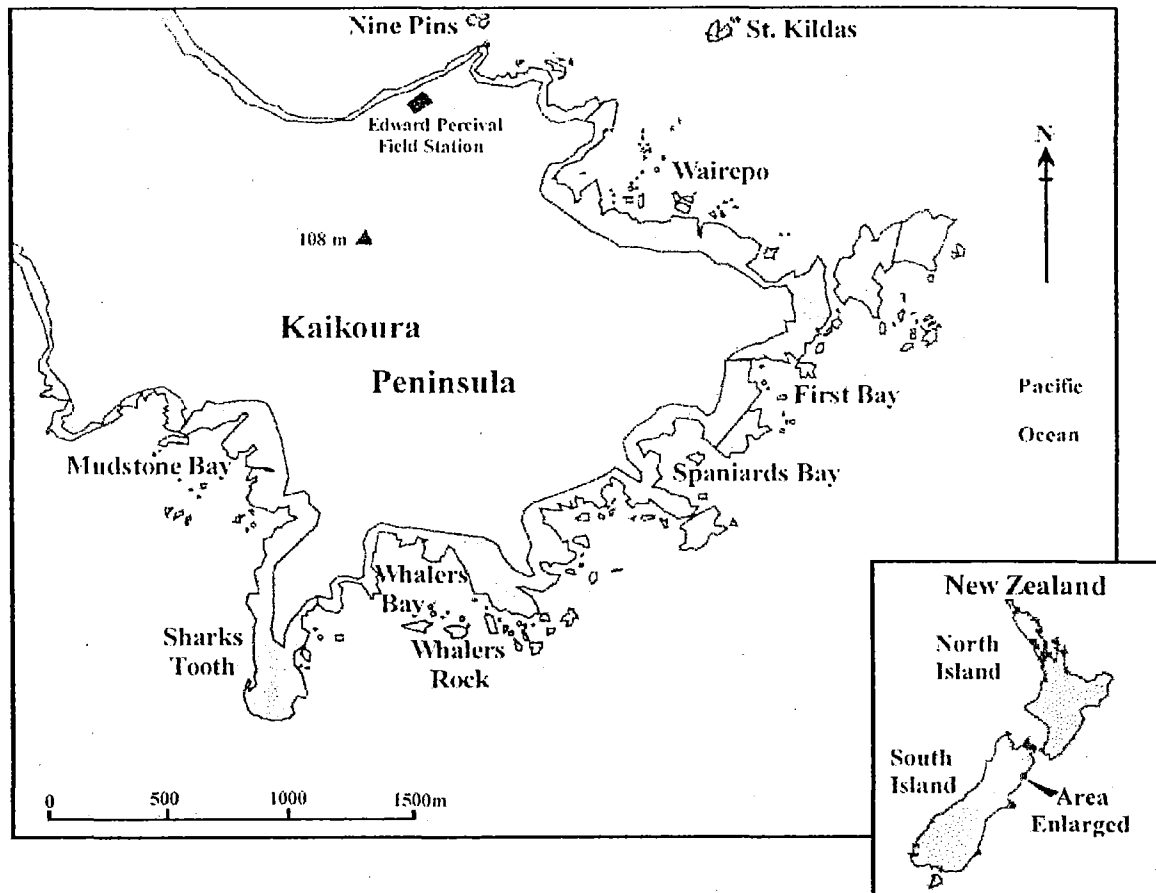


Figure 1.1 Map of the Kaikoura Peninsula showing study sites with an inset depicting its location in New Zealand.

of subantarctic surface waters (Heath, 1970). In summer the absence of southerly winds means that the sea temperature may rise due to the introduction of warm tropical water from the East Cape Current (Heath, 1972). Kaikoura is classified as having cold temperate mixed waters with an annual mean fluctuation typical of New Zealand ranging from 8°C to 18°C (Davison & Van Berkel, 1985).

The Kaikoura coastline is exposed to high energy oceanic swells and storm waves. The wind is predominantly southerly in winter and northeasterly in summer (Rasmussen, 1965). The south side of the Peninsula generally receives the rougher seas and stronger winds, particularly in autumn and winter. These conditions, combined with oceanic currents and river outflow, means that there is often a distinct nearshore band of murky water.

CHAPTER TWO

DEMOGRAPHY AND DISTRIBUTION

2.1 INTRODUCTION

Temperate rocky reef environments support a wide variety of fish species that are dependent on the reef substratum, macroalgae and associated invertebrates for food and shelter. Many studies have investigated the association between the spatial and temporal distribution and abundance of fish among different habitats (Schiel *et al.*, 1986; Choat & Ayling, 1987; Choat *et al.*, 1988; Kingsford *et al.*, 1989; McCormick, 1989a; Fowler, 1990; Holbrook *et al.*, 1994). However, most studies of reef fish in New Zealand have been based in northern New Zealand where habitats differ ^{from} to those of the South Island. One major habitat missing in most of southern New Zealand is the large echinoid-dominated areas common in northeastern New Zealand. These echinoid-dominated areas that occur in areas of moderate exposure in the 4 - 10 m depth zone are reduced to small patches around Kaikoura (Schiel, 1990). Furthermore, there are differences in the structure of northeastern and South Island algal forests (Choat & Schiel, 1982; Schiel & Foster, 1986). In northeastern New Zealand laminarian algae, such as *Ecklonia radiata*, dominate to depths of at least 10 metres, whereas in the South Island fucoids, in particular *Marginariella boryana*, tend to dominate the shallow subtidal zone.

The general pattern of fish distribution in New Zealand is modified by ocean currents (Francis, 1996), which may influence the composition of the fish fauna. For example, the East Auckland current brings subtropical fishes to northern New Zealand (Schiel *et al.*, 1986), whereas the subantarctic Auckland Islands have a distinct subantarctic fauna (Kingsford *et al.*, 1989). South Island reef fish assemblages are likely to differ from the North Island in terms of both species diversity and biomass. For example, of the 120 species described by Francis (1988), 108 occurred along the northeast coast of the North Island. The abundance of reef fish and associations with habitat have only been cursorily described in the South Island (Hickford, 1993; Hickford & Schiel, 1995).

Fish numbers vary significantly over a wide range of temporal and spatial scales in tropical (Choat & Bellwood, 1985), subtropical waters (Schiel *et al.*, 1986), temperate (Russell, 1977; Leum & Choat, 1980; Kingett & Choat, 1981; Choat *et al.*, 1988; Holbrook *et al.*, 1994), and subantartic waters (Kingsford *et al.*, 1989). Temporal variability appears to depend on the species or populations concerned, but in general, the composition and abundance of fish assemblages appear to be fairly constant over time (years) (Ebeling *et al.*, 1980; Kingett & Choat, 1981; Stephens & Zerba, 1981; Jones, 1984c; McCormick, 1989a; DeMartini & Roberts, 1990; Holbrook *et al.*, 1994). For example, the large reef fish *Cheilodactylus spectabilis* exhibited similar abundance patterns within sites in studies seven years apart (Leum & Choat, 1980; McCormick & Choat, 1987). Similarly, densities of sheephead wrasse, *Semicossyphus pulcher*, did not vary significantly among reefs in California (Holbrook *et al.*, 1990) and Jones (1984c) reported that densities of *N. celidotus* varied more between sites and habitats than among years.

The physical and biological characteristics of a reef habitat, such as topographic complexity, substrate type, and algal cover appear to have a major influence on the distribution and abundance of reef fishes (Russell, 1977; Willan *et al.*, 1979; Kingett & Choat, 1981; Jones, 1984a, b, c; Choat & Ayling, 1987; Levin, 1993; Carr, 1994). Studies that have examined the distribution of fish across reef environments have found that structurally complex reef habitats support a larger and more diverse fish assemblage than less complex environments (Alevizon & Brooks, 1975; Luckhurst & Luckhurst, 1978; Hixon, 1980; Leum & Choat, 1980; Kingett & Choat, 1981; Jones, 1984a, b; Moreno & Jara, 1984; Choat & Ayling, 1987; Behrents, 1987; Bodkin, 1988; Carr, 1991; Connell & Jones, 1991; Lincoln-Smith & Jones, 1995). Areas of greater topographic complexity provide a greater diversity of available shelter both for recruits and adult fish, and a corresponding increase in algae and associated invertebrates on which many reef fish feed.

Temperate reefs in New Zealand are characterised by macroalgae that can exhibit substantial variation both spatially and temporally (Choat & Schiel, 1982; Schiel and Foster, 1986). This variation can strongly influence the species abundance and composition of reef fish (Hobson, 1972; Ogden & Ehrlich, 1977; Jones, 1984c; Larson & DeMartini, 1984; Carr, 1989, 1991; DeMartini & Roberts, 1990) because reef fish, particularly juveniles, often have a close association with macroalgae (Jones, 1980, 1984c; Choat & Ayling, 1987; Holbrook *et al.*, 1990; Carr, 1991; McCormick, 1995). Macroalgae provide sources of food (Jones, 1984b; Schmitt & Holbrook, 1986; Carr, 1991), shelter (Ebeling & Laur, 1985; Behrems, 1987; Choat & Ayling, 1987; Anderson, 1994), recruitment habitats (Choat, 1982; Jones, 1980; Holbrook & Schmitt, 1988) and spawning sites (Jones, 1984a; Choat & Ayling, 1987; Holbrook *et al.*, 1994). The removal of kelp can affect fish abundance and density (Carr, 1989, 1994). Bodkin (1988) detected a reduction in the density and abundance of fish species when one hectare of kelp forest was experimentally cleared. Jones (1984b) and Levin (1993) found that the removal of kelp caused a decrease in the densities of juvenile *N. celidotus* and *Tautoglabrus adspersus*, respectively. Conversely, other workers have found that the presence or absence of kelp had little effect on the abundance of local fish assemblages (Stephens *et al.*, 1984).

The trend for increasing size with depth appears to be a common feature of many fish species (Olla *et al.*, 1974; Johannes, 1978; Jones, 1981; 1984c; Choat & Ayling, 1987; McCormick, 1989a; Kingsford *et al.*, 1989; Green, 1996; Gillanders, 1997), with the distribution of small and medium sized fish being quite different from that of larger adults (Williams & Hatcher, 1983; Choat *et al.*, 1988). For example, large *Achoerodus viridis*, *N. celidotus* and *Cheilodactylus spectabilis* tend to be more abundant in deeper waters, whereas shallow water habitats consist mainly of smaller fish (Choat, 1965; Jones, 1984a; McCormick, 1989a; Gillanders, 1995a). Variations in the densities of fish between different depths may be due to recruitment occurring in shallow water followed by a gradual outward migration with increasing size (Leum & Choat, 1980; McCormick, 1989a; Levin, 1991; Gillanders, 1997). Olla *et al.* (1974) suggested

that ontogenetic habitat differences functioned in reducing both predation and intraspecific competition. Choat & Ayling (1987) attributed differences between the differing sizes of fish found on algal dominated areas and reef flats to differences in preferred prey items.

Many temperate fishes exhibit cycles of small-scale, seasonal movements that relate to water temperature change, climatic change, and algal die-off (Kuwamura, 1981; Helfman *et al.*, 1997). Many benthic species require cool water and are only common when water temperatures remain below a threshold (Stephens *et al.*, 1984). Stephens *et al.*, (1984) related the reduced number of some benthic fishes to an influx of warm water into California. A seasonal disappearance has been suggested for wrasses living in colder temperate waters. Seasonal water variation may force residents into deeper waters to avoid environmental extremes (Kuwamura, 1981), or cause them to hide in a state of torpor (Roede, 1972; Olla *et al.*, 1979). Winter migration to deeper waters has been reported for *Labrus ossifagus*, *Coris julis*, *Xyrichthys novacula* (Roede, 1972), and *N. celidotus* (Choat, 1962). Graham (1956) recorded that Otago Harbour became almost devoid of *N. celidotus*, *N. fucicola* and *Pseudolabrus miles* in winter. Conversely, Barrett (1995a) found that the six temperate species he studied remained present and active throughout the year, which he attributed to the small seasonal water temperature variation of 8-18°C.

The El Nino-Southern Oscillation is a large cyclical (3-7 year) warming and cooling episode across the equatorial Pacific (Glynn, 1990). The 1997 - 1998 El Nino event affected many marine species around Kaikoura. A high mortality rate of many invertebrates, including sea urchins (*Evechinus chloroticus*), yellowfoot paua (*Haliotis^o australis*), crayfish (*Jasus edwardsii*) and *Octopus maorum* was reported over the summer. This mortality was linked to toxic algae, the occurrence of which was likely to be associated with large scale changes in oceanographic conditions in the region, especially the intrusion of warmer subtropical water further south than usual (Anon, 1998).

The settlement of *N. fucicola* is expected to be similar to that of *Notolabrus celidotus*, occurring over a three month period from early December to late February. Juvenile *N. celidotus* (30 - 40 mm) were found in seaweed during this period (Jones, 1984b). However, Duffy (1989) sampled inshore macroalgae around Kaikoura subtidal areas and found that, even where juvenile *N. celidotus* were abundant, there were no juvenile *N. fucicola*, suggesting that *N. fucicola* do not recruit into shallow macroalgae or that their recruitment is more variable.

Labrid fishes are conspicuous members of reef fish assemblages on temperate reefs in different parts of the world, yet there is a paucity of information on their abundance patterns at different temporal and spatial scales. In New Zealand the spatial and temporal patterns between the spotty, *Notolabrus celidotus*, and its habitat has been described by Jones (1980, 1981, 1984a, b, c). Spatial relationships have been cursorily described for *Notolabrus fucicola* in northeastern (Choat & Ayling, 1987) and southeastern New Zealand (Hickford, 1993; Hickford & Schiel, 1995).

The main aim of this chapter is to investigate spatial and temporal variation in the distribution and abundance of *N. fucicola* and associated reef fishes around Kaikoura, in particular, the association of fish densities ^{with} between depths, among sites, and over time.

2.3 METHODS

2.3.1 STUDY SITES

To examine the fluctuations in numbers of reef fish populations over time and depth, nine sites around the Kaikoura Peninsula were surveyed monthly for thirteen months from December 1996 to December 1997. For a map of the study area and site locations see Figure 1.1.

As Hickford (1993) has examined associations of reef fish with habitat around Kaikoura it was not necessary to investigate spatial patterns. Instead temporal patterns and associations with depth were examined. The nine sites were grouped into three depths, 0-6 m, 7-11 m and 12-18 m. Reefs around Kaikoura are more vertical and do not gradually slope as do the shores of northern New Zealand reefs. For example, many reefs in northern New Zealand slope gently to a depth of 25 m some 350 m offshore (McCormick, 1989a). Because of this it was difficult to sample three depths within one reef. Therefore, sites were not orthogonal to depth in my study.

The habitat at each site was determined in November 1996, prior to fish counts. Fiberglass measuring tapes, 30 metres long, were laid out in randomly selected areas at each site. A diver swam along and recorded the seaweed cover, individual seaweed abundance and substrate type within 4 m² at random intervals (determined from a random number table) five times per transect. Five transects were done per site. Sites varied from < 0.1 km apart to 2 km apart. Each site was marked with a buoy to ensure accurate relocating (Table 2.1).

*Reefside
for fish
counts?*

Table 2.1 Summary of characteristics of the nine sites sampled over the study (SW = seaweed).

Site	Depth	Habitat description	Main seaweed	SW %
Mudstone Bay	0-6m	Rocky mudstone reef consisting mainly of unbroken bedrock.	<i>Carpophylum mashalocarpum</i>	80
Wairepo	0-6m	Rocky mudstone reef with large rocks and sandy areas.	Mixed algae	88
Whalers Bay	0-6m	Shallow broken reef with many large rocks.	Mixed algae	89
First Bay	7-11m	Rocky reef with irregular ridges and gullies.	<i>Marginariella boryana</i>	58
Sharks Tooth	7-11m	Rocky reef with large rocks and channels.	Mixed algae	56
Spaniards Bay	7-11m	Sheltered rocky reef. Many scattered smaller rocks.	<i>Carpophylum mashalocarpum</i>	56
Nine Pins	12-18m	Offshore rocks with an irregular bedrock bottom.	<i>M. boryana</i>	25
St. Kildas	12-18m	Offshore limestone rock and cobbles.	<i>M. boryana</i>	36
Whalers Rock	12-18m	Sloping rocky reef with irregular ridges and gullies.	Mixed algae	22

2.3.2 SAMPLING DESIGN

Reef fish ecologists frequently make use of visual census techniques for determining the abundance and diversity of fish present in an area (Brock, 1954; Jones & Chase, 1975; Jones, 1980; Lincoln-Smith, 1989). The purpose of a visual census is to obtain an accurate estimate of the numbers of each species present at a site without disturbing the assemblage or by taking a destructive sample, such as trapping, trawling, poison or explosives (Leum & Choat, 1980; Sale & Douglas, 1981; Sale & Sharp, 1983). There are, however, problems associated with visual counts. These include observer variability and experience, swimming speed, species identification and data recording (Keast & Harker, 1977; Jones & Thompson, 1978; Brock, 1982; Sale & Sharp, 1983; Bortone *et al.*, 1986; Lincoln-Smith, 1988; McCormick & Choat, 1987). These problems were accounted for in this study. Exercises in recognising and

recording fish species and estimating standard lengths were done in November 1995 around Kaikoura. The lengths of reef fish were estimated, then fish were caught by spearing to verify estimates. Small cryptic fish, for example, triplefins and blennies, which are often underestimated were omitted from counts. Underwater visibility is a critical factor influencing data collection using sampling transects (Bortone *et al.*, 1986). Therefore, transects were only undertaken when visibility was > 2.5 metres. All studies using the visual census technique have pointed out the problems and shortcomings of this technique but all have accepted the method as it seems to be the most effective non-destructive method of surveying reef fish populations, especially where sites are re-visited through time.

Transect counts were carried out following the basic design described in Hickford (1993). Two divers descended to the substrate, one diver swam a thirty metre fiberglass tape out, attached one end to a seaweed holdfast, returned to the beginning of the tape, ascended for approximately two minutes (to allow the substrate to settle and labrids to disperse), then began the transect. Fish counts were made while two divers swam along either side of the tape at a constant speed one metre above the substratum, each recording the standard length (from snout to the base of the tail) of all fish sighted two and a half metres to the side of the line (all lengths given in this thesis are standard length). Any fish that crossed the tape were assumed to have already been recorded by the other diver. All fish were recorded on perspex slates which contained the names of 11 species, plus space for additional ones. The date, time of day, water visibility, depth and habitat were recorded. Water temperature was recorded at the conclusion of the final transect. The 30 m transect length was used as this length has been found to be the most effective within the constraints of the time and effort available (McCormick and Choat, 1987; Hickford, 1993). Five replicate transects were laid at random within each reef at each sample time, providing a mean estimate of density per 150 m². Observations were made between 0800 and 1400 hours.

The frequency of occurrence of all reef fish observed and temporal changes in the four most common species in the nine study sites were described and graphed. More detailed analysis were done for *Notolabrus fucicola*, *N. celidotus* and *Odax pullus*. An analysis of variance was done to assess the effects of time and depth on the numbers of *N. fucicola*, *Odax pullus* and *N. celidotus*. Also, an ANOVA was done to assess the effects of *N. fucicola* size across time and between depths. Data were tested for homogeneity of variances using Cochran's test prior to analysis and data were transformed when necessary. All data were transformed using $\log(x+1)$. In some cases variances could not be stabilised so a critical significance level of $p = 0.01$ was used to lessen the chances of a Type 1 error. This was the case for most analyses, except for numbers of *Odax pullus*. Analysis were done using Statistica 5.0 (Statsoft Inc.).

2.4 RESULTS

Eleven species of fish were recorded during the 845 transects of nine sites, over thirteen months, around the Kaikoura Peninsula (Table 2.2). These fish comprise an assemblage of non-cryptic benthic-feeding species which included both herbivores and carnivores. Relatively few species were recorded in each transect (150 m²), ranging from an average of 3.9 \pm 0.2 to 5.9 \pm 0.3 (all numbers stated after means are standard errors). There was a trend towards increasing species richness with increasing depth (Figure 2.1).

Table 2.2 Summary of species, their common name and code, observed over the study period.

Family and species	Common name	Code
Labridae		
<i>Notolabrus fucicola</i>	Banded wrasse	BPF
<i>N. celidotus</i>	Spotty	STY
<i>N. cinctus</i>	Girdled wrasse	GPF
<i>Pseudolabrus miles</i>	Scarlet wrasse	SPF
Odacidae		
<i>Odax pullus</i>	Butterfish	BUT
Latridae		
<i>Latridopsis ciliaris</i>	Blue moki	MOK
Pinguipedidae		
<i>Parapercis colias</i>	Blue cod	BCO
Aplodactylidae		
<i>Aplodactylus arctidens</i>	Marblefish	GTR
Balistidae		
<i>Parika scaber</i>	Leatherjacket	LEA
Cheilodactylidae		
<i>Cheilodactylus spectabilis</i>	Red moki	RMO
<i>Nemadactylus macropterus</i>	Tarakihi	TAR

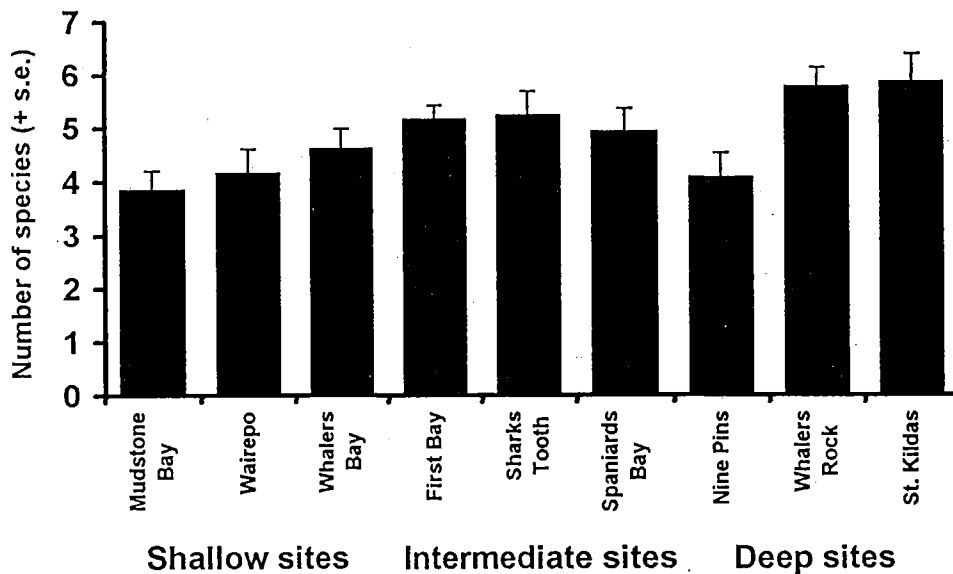


Figure 2.1 Mean number of species observed per transect (150 m²) (+ s.e.) in each of the nine sites at three depths (0-6 m, 7-11 m and 12-18 m) from Dec 1996 to Feb 1998 (65 transects per site).

Notolabrus fucicola and *N. celidotus* were the most abundant fishes at all sites, followed by *Odax pullus* and *Latridopsis ciliaris*. The remaining species were recorded in substantially lower numbers. For example, only one red moki, *Cheilodactylus spectabilis* was recorded at the deep St. Kildas site. Except for *Nemadactylus macropterus*, all other species became more abundant with increasing depth. These include *Parapercis colias*, *Notolabrus cinctus*, *Pseudolabrus miles* and *Parika scaber*. In fact, *P. scaber* were restricted to deep offshore rocky reefs, Nine Pins and St. Kildas (Figure 2.2).

N. fucicola numbers were lowest at the shallow sites, Mudstone Bay (1.6 ± 0.3) and Wairepo (2.2 ± 0.2), but also in the deep Nine Pins site (2.6 ± 0.5). All other sites recorded similar mean numbers ranging from 4.5 ± 0.6 to 6 ± 0.8 (Figure 2.2). Analysis of variance, as expected, showed significant differences in the numbers of the three most common species across sites (nested in depth): *N. fucicola* ($F_{1086,24} = 31.151$, $p < 0.001$), *N. celidotus* ($F_{1086,24} = 10.366$, $p < 0.001$) and *O. pullus* ($F_{1086,24} = 25.477$, $p < 0.001$) (Table 2.3, 2.4, 2.5).

Sample
size

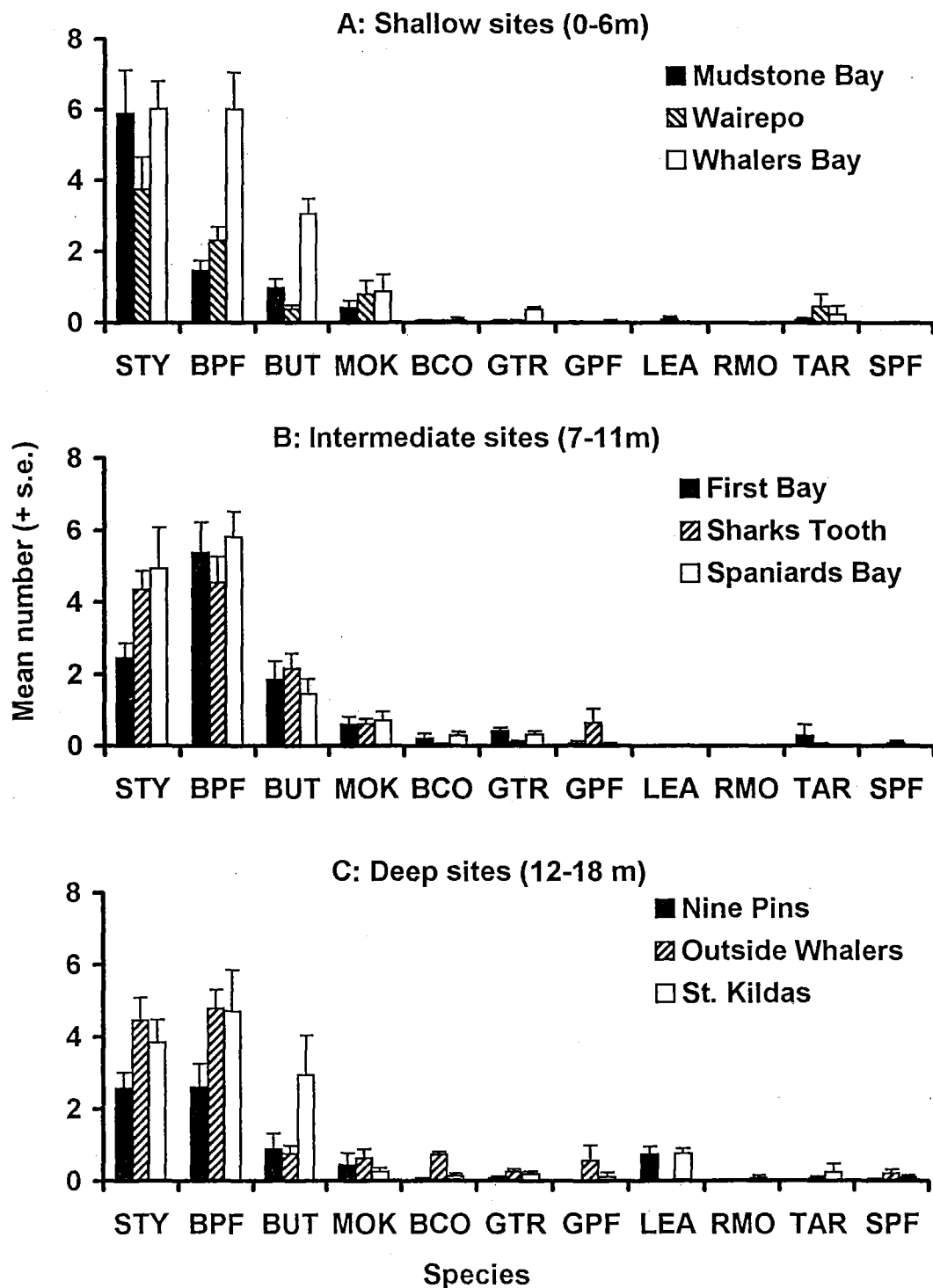


Figure 2.2 Mean number of eleven species of reef fish observed per transect (150 m^2) ($n = 65$) from Dec 1996 to Dec 1997 around Kaikoura at nine sites at three depths (+ s.e.). A: Shallow sites 0-6 m, B: Intermediate sites 7-11 m, C: Deep sites 12-18 m. See Table 2.2 for species codes.

There was little variation in *L. ciliaris* abundance with depth but it appeared *N. celidotus* decreased in abundance with increasing depth. At intermediate depths *N. fucicola* and *O. pullus* had the greatest abundance (Figure 2.2). However, an analysis of variance revealed no significant difference between fish numbers with depth for the three common species, *N. fucicola* ($F_{1086,24} = 1.359$, $p = 0.326$) (Table 2.3), *N. celidotus* ($F_{1086,24} = 1.281$, $p = 0.344$) (Table 2.4) and *O. pullus* ($F_{1086,24} = 0.224$, $p = 0.806$) (Table 2.5). Analysis of variance established that there were no significant interactions between time and depth for all three species; *N. fucicola* ($F_{1086,24} = 1.677$, $p = 0.049$) (Table 2.3), *N. celidotus* ($F_{1086,24} = 1.353$, $p = 0.164$) (Table 2.4) and *O. pullus* ($F_{1086,24} = 1.303$, $p = 0.195$) (Table 2.5).

Table 2.3 Analysis of variance on the effects of time, depth and sites on the numbers of *Notolabrus fucicola*; depth nested in site, sites treated as random factors: data $\log(x+1)$ transformed but remained heterogeneous after transformation (Cochrans $C=0.028$). A critical significance level of 0.01 was used.

Source of variation	df	MS	SS	F	p-level
Time	12	0.338	12.338	2.259	0.017
Depth	2	2.195	4.195	1.359	0.326
Sites (depths)	6	1.615	7.615	31.151	0.000
Time x Depth	24	0.251	24.251	1.677	0.049
Time x Site (depth)	72	0.149	72.149	2.882	0.000
Residual	1086	2.018	2191.013		
Total	1202				

Table 2.4 Analysis of variance on the effects of time, depth and sites on the numbers of *Notolabrus celidotus*; depth nested in site, sites treated as random factors: data $\log(x+1)$ transformed but remained heterogeneous after transformation. A critical significance level of 0.01 was used.

Source of variation	df	MS	SS	F	p-level
Time	12	6.230	18.230	3.398	0.001
Depth	2	7.037	9.037	1.281	0.344
Sites (depths)	6	5.494	11.494	10.336	0.000
Time x Depth	24	2.480	26.480	1.353	0.164
Time x Site (depth)	72	1.833	73.833	3.449	0.000
Residual	1086	10.224	11102.91		
Total	1202				

Table 2.5 Analysis of variance on the effects of time, depth and sites on the numbers of *Odax oullus*; depth nested in site, sites treated as random factors: data $\log(x+1)$ transformed to remove heterogeneity of variance (Cochrans C=0.98).

Source of variation	df	MS	SS	F	p-level
Time	12	0.391	12.391	2.205	0.020
Depth	2	0.325	2.325	0.224	0.806
Sites (depths)	6	1.454	7.454	25.477	0.000
Time x Depth	24	0.231	24.231	1.303	0.195
Time x Site (depth)	72	0.177	72.177	3.109	0.000
Residual	1086	1.923	2088.161		
Total	1202				

The number of fish recorded per transect each month depended on the site and time of year. There were fluctuations over time for the four main species, ^{but} these changes were irregular with no obvious seasonal patterns to density change. There were increased numbers observed in January and February at most sites but also peaks at other sites in June (Spaniards and Whalers Bay) and October (First Bay) (Figure 2.3). Analysis of variance showed significant variation in numbers over time for *N. celidotus* ($F_{1086,24} = 3.398$, $p = 0.001$) and *O. pullus* ($F_{1086,24} = 2.205$, $p = 0.02$) (Tables 2.4, 2.5). However, there was no significant difference in numbers over time for *N. fucicola* ($F_{1086,24} = 2.259$, $p = 0.017$) (Table 2.3). There were no obvious trends in the temporal abundance of *Notolabrus fucicola* at any sites (Figure 2.3).

There was a significant difference ^{in size?} observed between ^{size?} size and ^{depth?} depth for *N. fucicola* ($F = 6.148$, $p = 0.007$). Although there were significant differences in size across depth, ^{but} the general trend of increasing size with depth was not observed for *N. fucicola*. Instead the smallest fish were found in the intermediate sites. However, the variation in the average size of *N. fucicola* between sites was small, with only 2 cm between the largest and smallest mean size ^s (Figure 2.4).

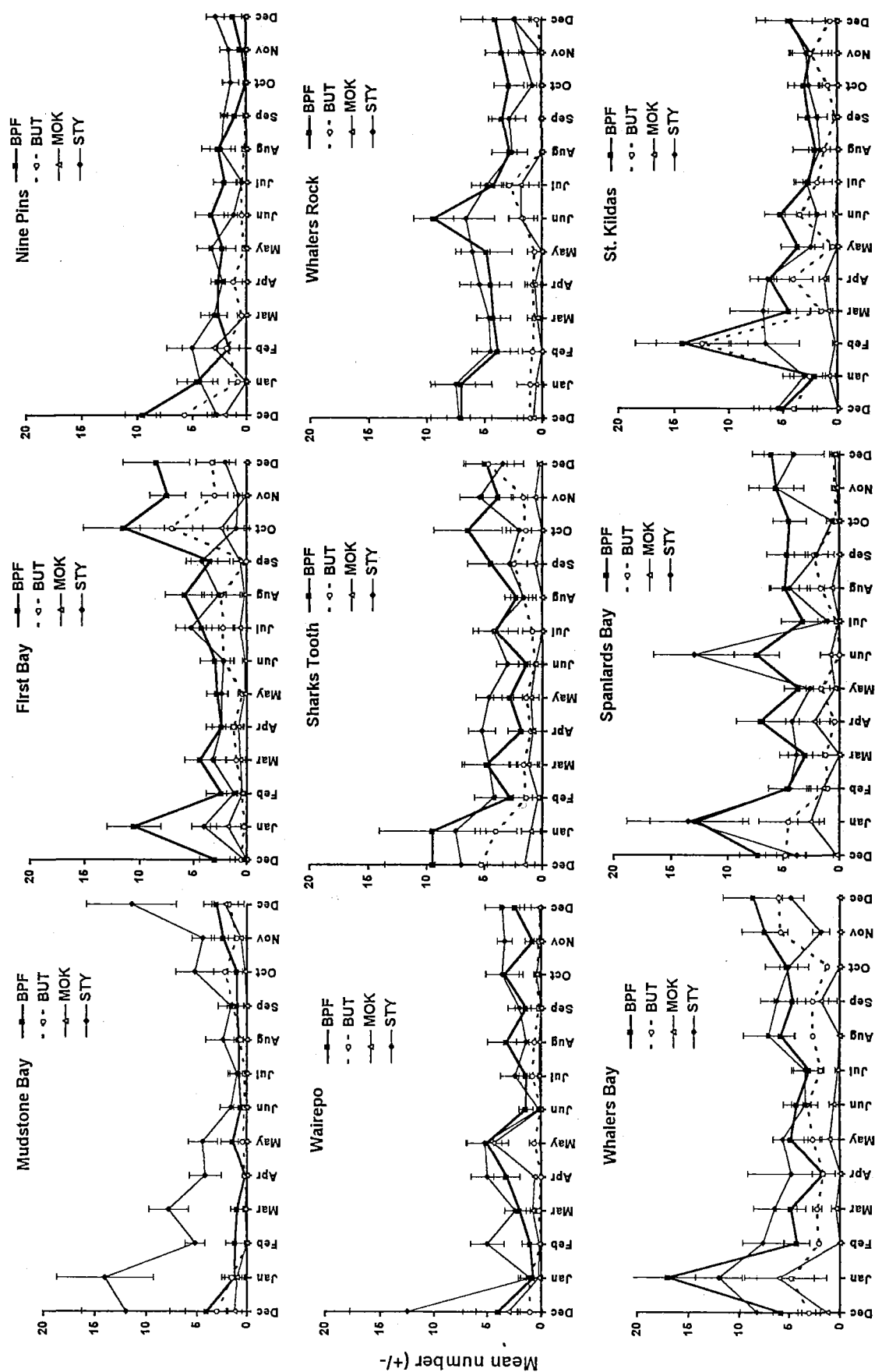


Figure 2.3 Mean number of fish per transect (n = 65) for four common reef fish at nine sites around Kaikoura from Dec 1996 to Dec 1997 (+/- s.e.). See Table 2.2 for species codes.

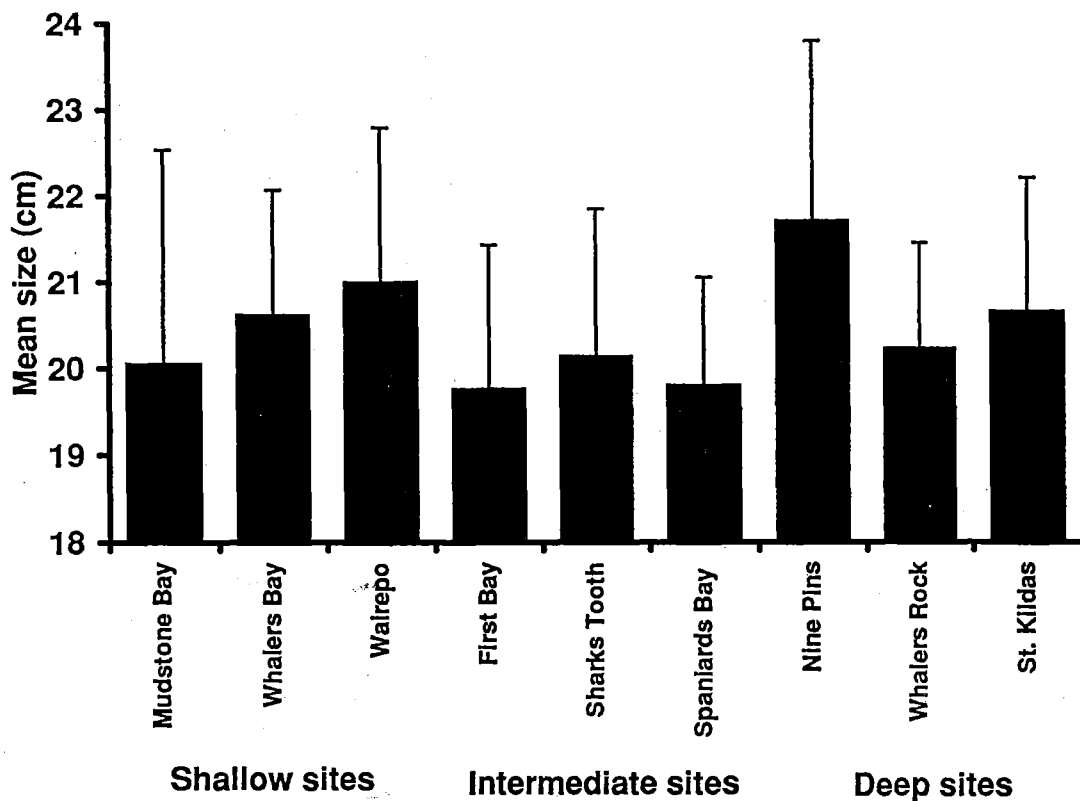


Figure 2.4 Mean size (cm) (+ s.e.) of *Notolabrus fucicola* at nine sites at three depths, shallow (0-6 m), intermediate (7-11 m) and deep (12-18 m), around Kaikoura from Dec 1996 to Dec 1997 (65 transects per site).

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 There was no significant variation in the size of *N. fucicola* across time ($F = 1.834$, $p = 0.01$). Graphing size changes of *N. fucicola* across time reveals a similar pattern for fish sizes at different sites. In general, similar sized fish were usually seen at most sites (Figure 2.5). Trends that may have been expected, but were not observed, were higher numbers of small recruits in February and larger fish migrating to deeper waters to spawn from July to December. Large fluctuations in fish size within the shallow sites of Mudstone Bay and Wairepo were due to the low numbers of fish observed at these sites over time (Figure 2.5A). The common trend in many labrids is for larger fish to be found in deeper areas. This was not found in this species which reflects the universal distribution of this species at all depths. Interestingly, the deep Nine Pins site had a low total density and the greatest mean size (see Figures 2.2c and 2.4). The significance of this will be discussed below.

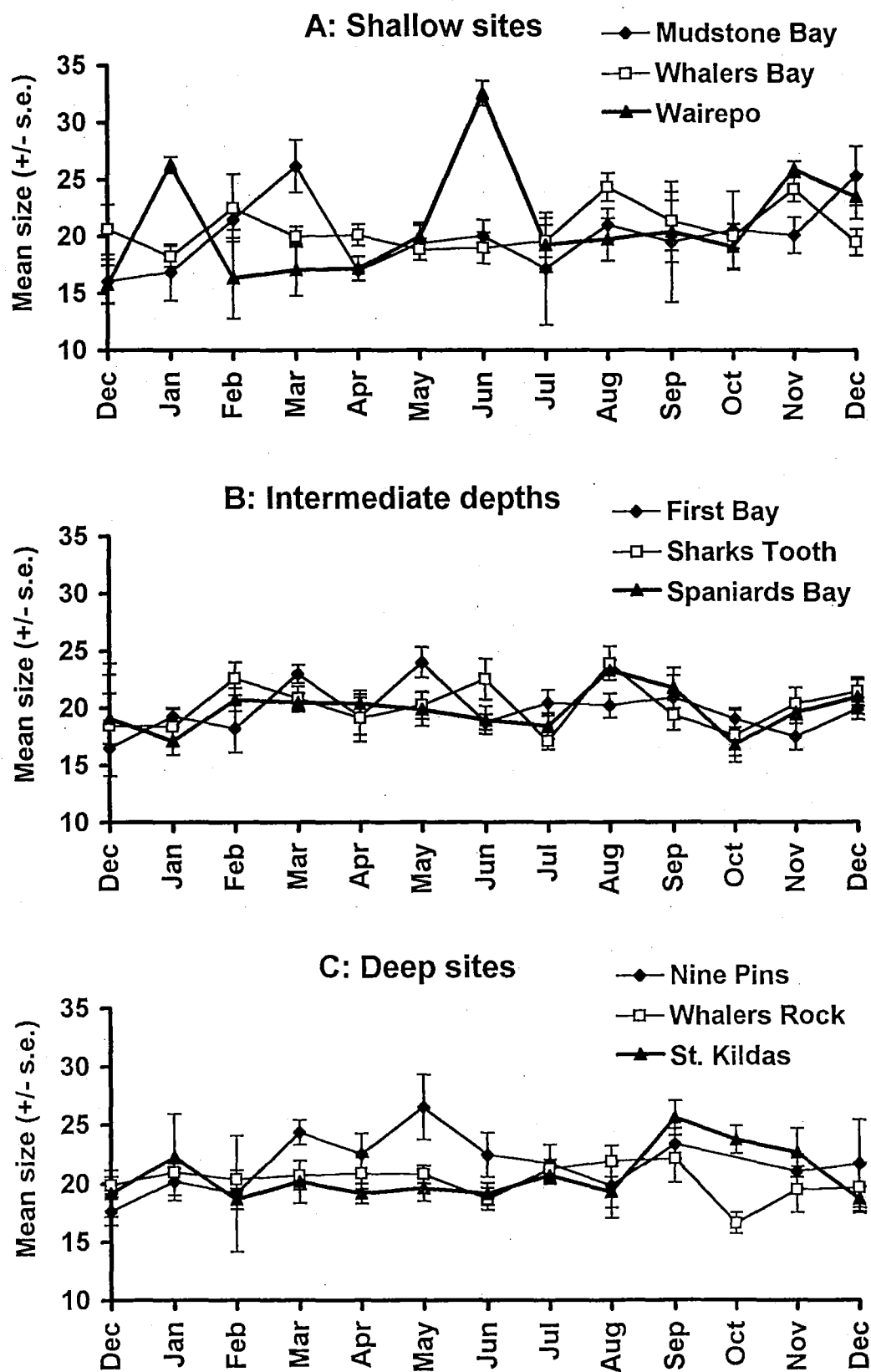


Figure 2.5 Mean size (cm) (+/- s.e.) of *Notolabrus fucicola* per transect (150 m²) around Kaikoura at A: Shallow sites (0-6 m), B: Intermediate sites (7-11 m) and C: Deep sites (12-18 m) from Dec 1996 to Dec 1997.

2.5 DISCUSSION

The biological and topographical differences between northeastern and southern habitats are reflected in differences in the number of reported species. Eleven species were recorded in both this study and Hickford & Schiel (1995) for the same region. In northern New Zealand Choat & Ayling (1987) recorded 22 species and Choat *et al.*, (1988) found 16 species in transects at the Poor Knight Islands. Choat & Ayling (1987) noted major differences in the species composition and abundance of reef fishes between northern New Zealand and Wellington and Francis (1996) reported that New Zealand fish species diversity decreased linearly with increasing latitude. Differences in species numbers are due mainly to the distribution of major water currents around New Zealand. For example, northern New Zealand has a strong subtropical influence (Ayling, 1982), whereas Wellington and Kaikoura are influenced by the colder Southland Current (Heath, 1972).

This study, as expected, found similar results to other authors investigating the spatial and temporal distribution of reef fishes (e.g. Jones, 1981, 1984c; Kingett & Choat, 1981; Choat & Ayling, 1987; McCormick, 1989a; Holbrook *et al.*, 1990, 1994; Hickford, 1993), with many of the resident reef fish species around Kaikoura associated with habitat type. These associations are primarily related to the feeding patterns of individual species. For example, the herbivorous butterflyfish, *Odax pullus* and marblefish, *Aplodactylus arctidens* are associated with algae. Unexpectedly, *O. pullus* was recorded in higher numbers at the deep St. Kildas site that has a relatively low percentage of algal cover (36%). Species that consume macroinvertebrates such as blue cod, *Parapercis colias*, and tarakihi, *Nemadactylus macropterus*, tend to avoid algal areas when foraging (Choat & Ayling, 1987). However, in my study they were recorded at all sites, suggesting a closer association with macroalgae than previously reported. *Parika scaber* were present in all northern New Zealand sites but were absent in Wellington (Choat & Ayling, 1987). Around Kaikoura *P. scaber* were recorded only on the deeper offshore reefs of Nine Pins and St. Kildas.

Labrids, particularly *Notolabrus fucicola* and *N. celidotus*, occur at all sites around Kaikoura. This is not surprising as these species are abundant throughout New Zealand from the Three Kings Islands to Stewart Island (Doak, 1972; Choat & Ayling, 1987). *N. fucicola* showed no significant difference in abundance across five habitat types around Kaikoura (Hickford, 1993). Other labrids, *N. cinctus* and *P. miles*, were found only in deeper water. In his review, Jones (1988) found that labrids with a southern distribution showed much less variation in numbers. Although Choat & Ayling (1987) found both Three Kings and Wellington supported similar densities of *N. fucicola*, Jones (1994) estimated the density of *N. fucicola* per 500 m² in Northern New Zealand was 2.6 +/- 0.6. The density of *N. fucicola* around Kaikoura was substantially higher averaging from 1.6 +/- 0.3 to 6 +/- 0.8 per 120 m² depending on the site, implying that *N. fucicola* are more abundant in the South Island.

150?

N. fucicola showed significant differences in numbers over time but no obvious patterns, with different habitats exhibiting peak and trough densities at different times. This is consistent with Jones (1984b) and Choat *et al.* (1988) who found similar results for both *N. celidotus* and *N. fucicola*. The peak in abundance of many species, at most sites, in January and February may be due to increased fish activity because of warmer waters. A peak in February at St. Kildas may have been due to an abundance of macroplankton that has been reported to occur at this site over the summer months (Fenwick & Marsden, 1981). Fish that have low total densities tend to have the greatest mean size (Jones, 1984c). This was the case for the deep Nine Pins site where the highest mean size of *N. fucicola* was recorded which may have been because this site had more preferred prey items.

Although there was no obvious seasonal pattern to fish numbers over time, there was a peak in numbers at most sites in January and February which may have coincided with the conclusion of the breeding season. Some species may have increased feeding activity during this period. Evidence for this comes from

the increased gut fullness and condition factor of *N. fucicola* during this period (See Figures 4.6 and 4.7).

The wide variation in the densities of reef fish between habitats is consistent with other studies examining abundance patterns in both temperate and tropical regions (Russell, 1977; Ebeling *et al.*, 1980; Kingett & Choat, 1981; Leum & Choat, 1982; Jones, 1984c; Choat & Ayling, 1987; Choat *et al.*, 1988; McCormick, 1989b). Differences in abundance at different spatial and temporal scales can be attributed to many factors, mainly macroalgal abundance, depth, and bottom topography. Other factors that may cause variation in fish numbers at different sites include environmental disturbances, nutrient availability, runoff from land, amount of suspended material, time of day and year, migration, exposure, water temperature and currents, El Nino events, accessibility to fishers and divers, and recruitment variability (Russell, 1977; Ebeling *et al.*, 1979; Holbrook *et al.*, 1994).

The 1977 and 1983 El Nino events affected the structure of reefs and reef fish populations in southern California (Holbrook *et al.*, 1994). The temporal change in fish numbers that occurred on these reefs was due to fluctuations in the abundance of giant macroalgae (Stephens *et al.*, 1984). These fluctuations are unlikely to occur on New Zealand temperate reefs as kelp here may be temporally more persistent than giant kelp. Even in the unusually warm weather that occurred the 1997/1998 summer, there was no noticeable die-off of macroalgae.

The low abundance and species richness of fish at the shallow Mudstone and Wairepo sites may be because they are subject to higher tidal fluctuations and higher exposure during storms than the other shallow site. Alternatively, differences may be a result of recruitment failures, as the limestone platforms may be unsuitable for larval settlement. Doherty (1983) proposed that adult populations are largely recruitment-limited and are determined by the availability of settling larvae. Moreover, the explanation for the reduced abundance at these two shallow sites could be attributed to recreational

fishing. These areas are easily accessible to divers and fishers, who tend to capture butterflyfish. The numbers of butterflyfish between shallow sites were three times higher at Whalers Bay compared to the other two sites. Leum and Choat (1980) tentatively concluded that differences of fish abundance results in the more accessible shallow areas may be a result of human exploitation. Jennings & Polunin (1997) found that the biomass of all fishes differed significantly between areas of different fishing intensity in Fiji.

There was a significant difference observed in *N. fucicola* size with depth. However, the trend of increased size with depth was not observed. Instead the smallest fish were found at the intermediate sites. This is inconsistent with many studies that have found increasing size with increasing depth for many fish species (i.e. Jones, 1984a, McCormick, 1989a; Gillanders, 1995a). Barrett (pers. com.) reported that spawning aggregations of *N. fucicola* occurred in deeper waters (10 - 20 m). There was, however, no recorded movement of larger fish to deeper sites during the spawning period (August to December). Depth-related changes may not occur around Kaikoura as the habitat does not exhibit the marked change between macroalgae and barrens that occurs in the North Island. Kelp is present at all depths, although in smaller amounts with increasing depth, and barrens are confined to small patches (about 5 m²). These differences suggest that food and shelter associated with macroalgae are present at all depths. The outward migration with depth suggested by several authors for other labrids may not occur for *N. fucicola* because recruitment may not be restricted to shallow water. Duffy (1989) sampled inshore macroalgae around Kaikoura subtidal areas and found no juvenile *N. fucicola*. We saw several juvenile *O. pullus* and *N. celidotus* in shallow areas but only one *N. fucicola* <50 mm. The lack of sightings of juvenile *N. fucicola* in shallow areas and findings of Duffy implies that *N. fucicola* do not recruit into inshore algae but instead recruit into deeper waters. Furthermore, the smallest mean sizes of *N. fucicola* were recorded at the intermediate sites suggesting that recruitment may occur in these intermediate depths. Alternatively, the lack of sightings may have been because 1997-1998 may have been poor years for

recruitment, similar to Thompson's (1981) report that recruitment by *N. fucicola* into the Leigh Marine Reserve was extremely irregular in time and space.

The behaviour of fish can change daily and seasonally, accounting for some of the variation among samples over both short and long time scales. For example, *O. pullus* are reported to feed at high tide (Clements, 1985) so may be more visible during this period. E. Koops (pers. com.), a keen spearfisherman, noted that *O. pullus* were much easier to capture after they had been feeding after high tide. During the spawning season some species may become territorial and therefore more obvious. For example, territorial *N. fucicola* are more active than non-territorial fish, making them more conspicuous. Additionally, the peak in *N. fucicola* abundance in October, November and December at a few sites coincides with the spawning period.

It has been suggested that cold temperatures may influence the activity of reef fishes (Olla *et al.*, 1979; Stephens *et al.*, 1984; Helfman *et al.*, 1997). However, species recorded in this study remained present and active throughout the year. Barrett (1994) found that Tasmanian reef fish inhabiting a similar temperature range of 8 - 18°C were present year round. Fish that migrate to deeper water or go into a state of torpor may only do so when there are extreme variations in temperature.

Hickford & Schiel (1995) experimentally demonstrated that visual surveys and experimental gill-netting produced significantly different estimates of relative abundance of reef fishes and transient species. These differences were observed in this study as many species, not recorded in transects, were captured in gillnets set monthly. These were kawahai, *Arripis trutta*, red cod, *Pseudophycis bachus*, scorpionfish, *Scorpaena cardinalis*, trumpeter, *Latris lineata*, yellow-eyed mullet, *Aldrichetta forsteri* and black cod, *Paranotothenia magellanica*. Visual transects, therefore, do not sample all the fish using a reef, as many species are transient or occasional users.

CHAPTER THREE

LIFE HISTORY

3.1 INTRODUCTION

The life history, particularly the reproductive biology, of many labrids has been intensively investigated. This is because of a wide range of social systems exhibited by these fishes coupled with their complex life history patterns (Tribble, 1982). Chapter Three is divided into three general sections examining several aspects of the life history of *Notolabrus fucicola*. These are 1) reproductive biology, 2) reproductive seasonality, and 3) growth and age.

3.1.1 REPRODUCTIVE BIOLOGY

Among many teleosts sex change during their life history is a relatively common occurrence (Atz, 1964; Charnov, 1982). The reproductive patterns of tropical labrids have received extensive treatment (Roede, 1972; Robertson, 1972; Robertson & Choat, 1974; Warner, 1975a, 1984; Robertson & Warner, 1978; Warner & Robertson, 1978; Tribble, 1982; Warner & Lejeune, 1985). However, only a few authors have investigated the reproductive biology of temperate labrids. Those studied include *Notolabrus celidotus* (Jones, 1980, 1981a, 1984 a, b, c), *Archoerodus viridis* (Gillanders, 1995 a, b, 1997), *Centrolabrus exoletus*, *Crenilabrus melops* and *Ctenolabrus rupestris*, *Labrus bergylta* and *L. ossifagus* (Dipper & Pullin, 1979), *Pimelometopon pulchrum* (Warner, 1975b), *Semicossyphus pulcher* (Cowen, 1990), *Notolabrus tetricus*, *N. fucicola*, *Pictilabrus laticlavus* and *Pseudolabrus psittaculus* (Barrett, 1995a).

The most common reproductive pattern in the family Labridae is protogynous hermaphroditism, that is, the transformation from a functional female to a functional male (Warner, 1975a; Francis, 1992). In the southern hemisphere, the majority of temperate labrids investigated so far are protogynous hermaphrodites (see Thompson, 1981; Barrett, 1995a). This is in contrast to several northern hemisphere species that have been reported not to change sex. These include *C. exoletus*, *C. melops* and *C. rupestris* (Dipper & Pullin,

1979) and *Symphodus ocellatus*, *S. roissali*, *S. tinca* (Warner & Lejeune, 1985; Bentivegna & Benedetto, 1989).

There is confusion in the literature about the reproductive pattern of *Notolabrus fucicola*. Some authors have reported this species to be a protogynous hermaphrodite (Doak, 1972; Thompson, 1981; Ayling & Cox, 1987; Francis, 1988). For example, "*N. fucicola* can change sex any time after they first move permanently out of the plankton as small juveniles until they reach full adult size" (Francis, 1988). Conversely, Barrett (1995a) found *N. fucicola* in Tasmania to be secondary gonochorists that is, where all fish develop as females but males change before maturation so only function as a male or a female. Barrett explained that differences between New Zealand and Tasmanian populations could be explained by different evolutionary processes because of their physical isolation by distance.

Many workers have examined the adaptive significance of sex change in teleosts (Smith, 1967; Ghiselin, 1969; Warner, 1975a; Warner *et al.*, 1975; Charnov, 1982; Shapiro, 1984, 1993; Lejeune, 1987). The two main theories proposed to explain the phenomenon of protogynous hermaphroditism are the size advantage model and the social control model. Ghiselin's (1969) size advantage model states that protogynous hermaphroditism could occur when the reproductive prospects of functioning as the opposite sex exceeds the expectations of the current sex. Ghiselin (1969) wrote that "the size-advantage model would be the only available explanation for many instances of sequential hermaphroditism. This is especially true of shallow water marine fishes." This hypothesis implies that sex reversal is initiated by internal events physiologically related to body size, is genetically determined, relatively independent of external factors and similar for multiple populations of the same species (Choat, 1969; Roede, 1972; Warner, 1975a). This theory is supported by the fact that populations of most protogynous species are characterised by a sex-separated size distribution in which females predominate at small sizes and males dominate at larger sizes (Warner, 1975a; Jones, 1980; Shapiro & Lubbock, 1980; Shapiro, 1981a, b; Nemtzov, 1985). However, Sadovy &

Shapiro (1987) considered that biased sex distributions can indicate hermaphroditism but is not definitive evidence. Biased distributions may be due to completely different reasons such as differential growth or mortality rates, late sexual maturation of one of the sexes, or selective capture methods.

The assumption of the size advantage model that individuals change sex upon attaining a genetically predetermined size, is too restrictive to encompass the range of conditions under which sex change actually occurs (Shapiro, 1979, 1981a, 1984, 1987). Experimental evidence has demonstrated that social factors initiate sex change in many fishes, especially among fishes that live in harems (Fishelson, 1970; Robertson, 1972; Robertson & Hoffman, 1977; Hoffman *et al.*, 1985; Aldehoven, 1986) but also in some less organised social groups (Ross, 1983, 1990). Males may control production of other males by aggressive dominance over females (Fricke & Fricke, 1977) or sex change may be influenced by changes in group composition (Shapiro and Lubbock, 1980). There are many examples of socially controlled sex change where the removal of the dominant male causes the largest female to change sex. These include the Red Sea Razorfish, *Xyrichtys pendadactylus* (Nemtsov, 1985), *Labroides dimidiatus* (Robertson, 1972), *Anthias squamipinnis* (Fishelson, 1970; Shapiro, 1981b), *Thalassoma bifasciatum* (Shapiro, 1987; Warner & Swearer, 1991), *T. lucasanum* (Warner *et al.*, 1975; Warner, 1982), *T. duperrey* (Ross *et al.*, 1983; Ross, 1987) and *Thalassoma lunare* (Robertson, 1972; Fricke & Fricke, 1977). The wide variation in size at sex reversal for different populations at different sites demonstrates that circumstances inducing sex change do not occur at the same time of life for all individuals in a population (Warner, 1988)

There are many potential costs of sex reversal. These include metabolic expenditure to alter gonadal cell types (Shapiro, 1981), inducing new enzyme systems for biosynthesis of different steroid hormones, and changing colour pigments (Warner & Hoffman, 1980). There may also be a loss of growth and a loss of reproductive time if sex reversal occurs during the breeding season (Hoffman *et al.*, 1985). Moreover, there may be time delays involved in

attaining territorial male status. For example, male *Bodianus rufus*, *B. diplotaenia* and *T. bifasciatum* all had sustained periods following sex change during which their mating success was lower, on average, than both males and females (Hoffman *et al.*, 1985).

Sex change in temperate labrids is seasonal, typically being confined to the non-breeding period (Warner, 1975b; Dipper & Pullin, 1979; Jones, 1980) and is influenced by seasonal water temperature patterns. Some species, such as *T. duperrey*, are capable of changing sex year-round regardless of whether or not they are spawning (Ross, 1983). Sex change is characteristically rapid in many tropical species (Robertson, 1972). For example, *T. bifasciatum* and *Labroides dimidiatus* change sex very rapidly, with females initiating male behaviour, courtship and aggression, within hours after the removal of the TP males. Histological examinations showed these individuals had functional testes after 8 days (Roede, 1972; Warner & Swearer, 1991) and 14 - 18 days (Robertson, 1972) respectively. Sex change, in general, is usually not as extreme as these examples and can take 8 - 12 weeks, as in *Thalassoma duperrey* (Ross *et al.*, 1983).

An equal sex ratio can indicate gonochorism. For example, Warner (1975b) found an almost even sex ratio in the gonochoristic *Symphodus* species. In protogynous species the sex ratios tend to be strongly biased towards females (Sadovy & Shapiro, 1987). For example, *Archoerodus viridis* sex ratios ranged from 4: 1 to 62: 1 at different sites (Gillanders, 1995b). The female to male ratio in *Notolabrus celidotus* was 4.1: 1 (Jones, 1980).

Parental care and nesting are not a general characteristic among labrids (Roede, 1972), but does occur among some species, for example, *Crenilabrus melops* (Dipper & Pullin, 1979; Potts, 1984) and several *Symphodus* species (Bentivegna & Benedetto, 1989). Species that nest or display parental behaviour show little evidence of sex change as these factors can limit the reproductive success of large territorial males (Warner & Lejuene, 1985). This

is because competition is reduced between large and small males, reducing selection for sex change (Warner & Lejuene, 1985). In this system there is not the intense sexual selection in favor of large males that occurs with protogynous hermaphrodites (Bentivegna & Benedetto, 1989).

Two morphological types of males can exist for many labrids. A monandric population has only one type of male present (secondary), whereas a diandric population has two types of males present (primary and secondary) (Reinboth, 1967; Reinboth, 1970). Primary males are fish born as males while secondary males are sex-changed females (Sadovy & Shapiro, 1987). Primary males tend to be smaller and display the IP colouration whereas secondary males are larger and are associated with TP colouration. Because of this association with colour phases primary males are often called IP males and secondary males called TP males. The proportion of primary and secondary males is dependent on the population density (Warner *et al.*, 1975). Warner & Robertson (1978) found that labrids with abundant numbers had a lower proportion of TP males and a much higher proportion of IP males. It may not benefit IP males to change to a secondary male if the population density is high. For example, *Thalassoma lucanasum* lives in much higher population densities than *T. bifasciatum* and, although capable of changing sex and producing secondary males, rarely does so (Warner, 1982).

Many labrids exhibit a distinct demarcation between colouration and sex. In monochromatic species females are capable of developing all the same patterns as males. In dichromatic species females cannot do so and all the fishes of one colour phase are males (Warner and Robertson, 1978). Due to the variation in colouration in *N. fucicola* there are differing opinions about the association of colouration with sex, with some authors describing the sexes as being dichromatic (Doak, 1972; Francis, 1985) and others claiming that the sexes are monochromatic (Choat, 1962; Russell, 1988; Kuiter, 1993; Edgar, 1997).

Courtship is a series of behavioural actions performed by one or both members of a mating pair just prior to spawning. Courtship aids in species recognition,

attracting females, enticing females to spawn, pair bonding, orientation to the spawning site and synchronisation of gamete release (Tribble, 1982; Helfman *et al.*, 1997). Many labrid species perform ritualised swimming patterns or displays to attract females and these have been described as circling, looping, fluttering, dancing, or courtship swimming (Olla & Samet, 1977; Thresher, 1979; Tribble, 1982). For example, *N. fucicola* males constantly follow females during the spawning period, usually circling them and displaying raised dorsal and anal fins, until either being chased off by another male or swapping to another female (Ayling, 1980; Ayling & Cox, 1987; Barrett, 1995a).

The general mating behavioural strategies employed by labrids is generally either group or pair spawning. However, different labrid populations of the same species can have alternative mating strategies under different ecological conditions (Olla & Samet, 1977; Warner & Robertson, 1978; Pottle *et al.*, 1981; Turner, 1986; Shapiro *et al.*, 1994), a phenomenon known as behavioural scaling (Ross, 1990). For example, pair and occasional group spawning have been reported for *Tautoglabrus adspersus*, (Pottle, *et al.*, 1981), *Thalassoma bifasciatum* (Randall & Randall, 1963), *N. celidotus* (Doak, 1972; Jones, 1981a, b), *P. luculentus*, *P. miles* (Doak, 1972), *T. lunare* (Robertson & Choat, 1974), *Halichoeres maculipinna* (Robertson, 1981), *Labroides dimidiatus* (Robertson, 1972; Potts, 1974), and *Symphodus tinca* (Van Den Berghe, 1992). The presence of both group and pair spawning in some labrids allows for variation in the mating system according to the density and sex ratio of the local population. When the local population density is low pair spawning may be the most efficient way to ensure fertilisation, as large secondary males who can defend a territory will have a greater mating success than smaller primary males (Robertson & Choat, 1974; Tribble, 1982). Alternatively, on reefs supporting large breeding populations then group spawning may be the most effective breeding system, as the majority of secondary males will not be able to establish a mating territory (Robertson & Choat, 1974).

In a true protogynous system it would be expected that smaller males would have zero reproductive success as they would have few, if any, chances to spawn. Robertson & Choat (1974) suggested that a balance between primary

and secondary males exists because of a loosely organised social system. Such a system allows small IP males to exist undiscriminated against in the population and can compete with dominant males in the breeding season. These smaller males achieve reproductive success in three ways. 1) By interfering with normal pair spawning. For example, primary *T. bifasciatum* males attempt to sneak in and fertilise some of the eggs laid by the spawning pair and primary male *Symphodus quinquemaculatus* often rush in at the culminating point of courtship and release sperm (Roede, 1972). 2) By becoming 'sneakers' in that they mimic female colouration and behaviour. Primary male *Symphodus ocellatus* with female colouration, have large testes that causes a swelling of the abdomen. They may be mistaken for females and can rush in to fertilise any eggs present when the opportunity allows (Dipper & Pullin 1979). In New Zealand, Jones (1980) and Thompson (1981) reported instances of streaking by IP *N. celidotus* and *N. fucicola*, respectively. 3) By appearing in numbers too great for secondary males to defend (Roede, 1972; Robertson & Choat, 1974; Warner *et al*, 1975; Thresher, 1979; Warner & Robertson, 1978; Pottle & Green, 1979; Pottle *et al*, 1981; Warner, 1984; Nemtzov, 1985; Turner, 1986; Jobling, 1995).

3.1.2 REPRODUCTIVE SEASONALITY

The majority of fish species exhibit an annual reproductive cycle (Bye, 1984). The factors controlling the onset and duration of this cycle are not clear, but are likely to be controlled by an endogenous rhythm synchronized with environmental conditions (Bye, 1984; Helfman *et al.*, 1997). The environmental cues likely to trigger each stage of the reproductive cycle are changes in sea temperature, lunar cycles, current alterations and changing photoperiod. These changes are usually associated with seasonal, cyclical climatic events, such as oceanic surface and upwelling currents, and temperature cycles (Chan & Yeung, 1983; Helfman *et al.*, 1997). A seasonal reproductive cycle allows fish larvae to take advantage of greater planktonic productivity that occurs during spring and summer (Jillett, 1971; Robertson & Choat, 1974; Warner *et al.*, 1975; Sale, 1980; Ebeling & Hixon, 1991; Helfman *et al.*, 1997).

Labrids are often selective in spawning sites and times. The choice of spawning sites and times has been hypothesised either to minimise egg predation (Johannes, 1978), maximise dispersal (Barlow, 1981) or to provide maximum opportunity for pelagic larvae to survive with patchy and irregular distribution of food (Doherty *et al.*, 1985). Early spawning may be important for the growth and survival of larval and juvenile fish because of increased availability of food. For example, Jones & Thompson (1980) found that female *N. celidotus* had more spawning episodes early in the spawning season. Additionally, Pottle & Green (1979) found most of the spawning of cunner, *Tautogolabrus adspersus*, was concentrated early in the spawning season. However, there are no examples of fishes that show the advantages of early spawning on the survival of offspring (Jones & Thompson, 1980).

The formation of spawning aggregations at specific locations and times is a common mode of reproduction in some tropical reef families. Spawning times vary from early morning to soon after sunset in pelagic spawners (see references in Sadovy & Shapiro, 1987). Several labrid species move to deeper

waters to spawn, possibly to avoid egg-eating planktivorous fish that are more abundant in shallow areas (Warner *et al.*, 1975; Jones, 1980). The spawning rate of *N. celidotus* increased exponentially with the depth of the territory (Jones, 1981a, b). A review of pelagic spawning methods found contradicting results in relation to spawning locations, currents and times (Shapiro *et al.*, 1988). Several studies support the hypothesis that spawning locations are selected to maximise the rapidity of egg dispersal off reefs and minimise exposure to predators, whereas others do not support this hypothesis.

Spawning of most inshore temperate species is restricted to spring and summer (Jones, 1988; Kingsford, 1988; Ebeling & Hixon, 1991; Helfman *et al.*, 1997), in contrast to many tropical reef fishes which spawn year round (Ehrlich, 1975). The spawning season of *Notolabrus fucicola*, as in most temperate labrids, has been reported to be appropriately five months long, occurring from July until December (Doak, 1972; Jones, 1980, 1984a; Jones & Thompson, 1980; Robertson, 1980; Thompson, 1981; Kingsford, 1988; Barrett, 1995a). Water temperature appears to be an important factor influencing reproductive timing. *N. fucicola* eggs were first observed in coastal Otago plankton when the water temperature was at its minimum or shortly afterwards and were present over a temperature range from 9.2 - 10.6°C (Robertson, 1980).

Notolabrus fucicola, like most nearshore marine fishes, have planktonic eggs and larvae (Robertson, 1980; Russell, 1988), and hence their dispersal is closely tied to ocean currents (Olla & Samet, 1977; Johannes, 1978; Barlow, 1981; Doherty *et al.*, 1985; Cowen 1986). The eggs of *N. fucicola* were not observed to extend very far seawards (Robertson, 1973). In contrast, Leis & Miller (1976) found that the pelagic larvae of tropical labrids are nearly absent from inshore waters and are more common 3 km from shore, probably to avoid predators.

Labrids recruit during the summer months and are normally found on shallow rocky substrates with high algal cover (Roede, 1972; Levin, 1993; Carr, 1994;

Garcia & MacPherson, 1995). Variability of recruitment has been implicated as an important component structuring coral reef fish assemblages (Sale, 1980). However, little is known about the biological and physical processes that affect nearshore juvenile reef fish recruitment. These include 1) large scale processes that combine to affect the dispersal of larvae, such as the El Nino weather pattern, water temperature increases, and offshore tidal flows. For example, there was a large increase in the numbers of juvenile larvae in tropical Labridae during the 1982-1984 El Nino event (Glynn, 1990). 2) Small scale factors that influence the settlement of larvae, for example, substrate availability and topography, weed availability and depth and 3) factors predicting the survival of the settled larvae such as pre-emption of space by conspecifics and predation. Conspecifics can affect recruitment patterns in some species, but not in others, and at some locations, but not at others (Sale, 1977; Williams, 1980; Doherty, 1983; Shulman *et al.*, 1983; Jones, 1984a, 1987; Sweatman, 1985; Levin, 1993). Levin (1993) demonstrated "that the relative importance of settlement and post-settlement mortality or emigration varies among experimental habitats of different structures, and it is evident that a single process cannot adequately explain the population dynamics of different reef fish species or of populations of single species in different habitats."

3.1.3 AGE AND GROWTH

Little is known about the growth, age and size at maturity for *N. fucicola*. *N. fucicola* are reported to be relatively slow growing with an individual 300 mm long being about 10 years old and a large specimen probably being from 20 (Francis, 1996) to 25 years old (Ayling & Cox, 1987). These authors did not state the aging methods used. From otoliths, Barrett (1994) found a maximum age of 17 years.

Paul (1992), in a review of aging studies in New Zealand, found only a brief mention of measured growth in aquarium-held *N. fucicola* by Thomson & Anderton (1921) at the Portobello Marine Hatchery. *N. fucicola* can reach 120 mm at the end of their first year and they can mature during their second year at 180 mm (Francis, 1988).

The specific aim of this study was to investigate the reproductive biology and social system of *N. fucicola*. To find the onset of spawning and spawning duration, gonad changes were investigated over the study period. Additionally, to find size at sexual maturity and evidence for sex change, gonads were examined histologically. The relationships between sex, size and colour phases were also examined. Finally, I identified the relationship of size versus age, how long-lived this species is and how *N. fucicola* allocate their time.

3.2 MATERIAL AND METHODS

3.2.1 GENERAL METHODS

Thirty fish per month were collected over fifteen months (December 1996 to February 1998) to investigate the reproductive biology, seasonal variation, dichromatism, sex ratios, growth and age. Fish were collected using Hawaiian slings and fishing rods. Hawaiian slings were the preferred technique to collect samples as they enabled a representative size selection of fish to be taken from a population. Fishing rods were only used when spearing was not possible due to poor water visibility. Different sizes of hooks were used in an attempt to get an unbiased size range of fish. Fishing may be selective towards larger, more dominant males but this did not appear to be a problem in this study because all sizes were caught when using rods. The colour phase and sex of each fish were recorded, the standard length (SL) and total length (TL) measured to the nearest millimetre, and total weights recorded to the nearest gram. The gonads were removed, wet weighted, stored in Bouin's fixative for 48

hours then transferred to 70% alcohol for storage. To prepare for histological examination gonads were embedded in 'paraplast' paraffin wax, cut at 10 µm on a microtome, mounted on slides, stained in Ehrlich's Haematoxylin and Eosin and mounted in Eukitt.

In mature fish sex could be determined macroscopically because ovaries were rounded and granular and testes were smooth, convoluted and often milky. Gonads were obvious in all specimens examined indicating this species does not have degenerative gonads. For each individual a gonosomatic index (GSI) was calculated from the equation: $\text{gonad weight} / \text{total fish weight} \times 100$. The GSI is a calculation of the percentage of the body mass of the animal devoted to gonadal material (Helfman *et al.*, 1997). The effects of body size on gonad size are eliminated when the GSI is used.

Seasonal variations and differences between in the GSI values of male and female fish were tested for significant differences using ANOVA.

3.2.2 HISTOLOGY

N. fucicola gonads were examined histologically to determine if they are protogynous hermaphrodites and whether testes are primary or secondary in origin. Additionally, histology aimed to confirm visual identification of the sexes, identify the spawning period, identify primary or secondary males, and find if they are synchronous or successive spawners. The presence of a few unripe eggs in mature oocytes would indicate a synchronous spawner. If all stages of development are found then they are successive spawners (Dipper & Pullin, 1979; West, 1990).

Sadovy & Shapiro (1987) defined a species as hermaphroditic if a substantial proportion of individuals in a population possess functional testicular and ovarian germinal tissue, either simultaneously or sequentially, at any time. Hermaphroditism can only be detected through examination of large series of

specimens of varying life history stages taken from different times of the year (Reinboth, 1975). To identify sequential hermaphroditism in teleosts there are several anatomical features that strongly indicate prior female function. These are retention of the ovarian lumen and a lamellar form in testes, oocytic atresia, and multiple sperm ducts sinuses running longitudinally through the periphery of the gonadal wall (Warner, 1975; Dipper & Pullin, 1978; Ross, 1984; Nemtzov, 1985; Sadovy & Shapiro, 1987; Gillanders, 1995b).

Males are often excluded from gonad studies because they are generally more difficult to stage than females, may give a less well defined estimate of the spawning season, and do not show such large changes in gonad weight (West, 1990). My study examined male gonads mainly to find evidence of sex change or previous female function, size at maturity and if they were primary and secondary. Primary males generally have solid testes whereas secondary male gonads are either hollow, reflecting its origin as an ovary with a lumen, or solid but surrounded by a membrane derived from the ovarian wall (Sadovy & Shapiro, 1987).

There are considerable differences in the nomenclature concerning the various developmental phases of teleost gonad development. The terminology adopted here is from Dipper & Pullin (1979) and Takashima & Hibiya (1995). The developmental stages for each respective sex are listed and described below. Also included are other relevant tissue types that occur in the gonad (Tables 3.1 and 3.2).

Table 3.1 Summary of the stages of oocyte development

STAGES	CHARACTERISTICS
Pre-vitellogenesis	
Primary oogonia	These are small cells found along the edge of the trabeculae.
Chromatin nucleolus stage	Newly formed oocyte with a large nucleus.
Vitellogenesis	
Stage 1	Vitellogenic oocytes are characterised firstly by their larger sizes, the presence of many small scattered lipid droplets, and by the appearance of the chorion as a thin membrane between the cytoplasm and the follicle cells. The nucleus frequently has an irregular outline.
Stage 2	Cytoplasm filled with yolk vesicles and globules. The yolk develops peripherally until it fills the oocyte. The chorion may appear layered.
Mature	Complete development involves a rapid increase in oocyte diameter with a consequent thinning of the chorion that loses its two-layered appearance. The yolk now forms a homogenous mass
Post-ovulatory follicles (POF)	Distinctive convoluted mass of hypertrophied granulosa. No nuclear material is observed in POF.
Atretic oocytes	Atretic oocytes have a thin, irregular chorion and the cell contents appear disorganised, often spilling into the cytoplasm.

Table 3.2 Summary of the stages of male spermatogenic development

STAGE	CHARACTERISTICS
Spermatogonia	Darkly stained nuclei along the trabeculae. Observed as a large oval cell with a large clear nucleus.
Spermatocytes	Observed as large dark dots that cluster around the trabeculae. The nuclear membrane disappears.
Spermatozoa	Spermatocytes undergone spermatogenesis. Spermatids are present as purple streaks.
Mature testes	Mature sperm collecting and about to be released.
Melano-macrophage centres (MMC)	Brown atretic bodies that help to absorb sperm not released.

3.2.3 AGE AND GROWTH

Estimation of age from calcified tissue has been widely used in fisheries science (Weatherly and Gill, 1987). Growth increments are recorded within calcified bony structures of teleost fish, such as, scales, otoliths (ear stones), and vertebral bones. Scales can be the most useful method of aging temperate fish. Scale growth is accelerated in summer and retarded in winter, causing the formation of a dark band on the scale called an annulus (Bone *et al.*, 1995; Helfman *et al.*, 1997). However as fish age they have fewer original scales remaining.

To age *Notolabrus fucicola* both scales and otoliths were removed during dissection. At least six scales were removed from behind the left pectoral fin and stored in envelopes. The advantages of using scales from the pectoral

region are as follows: 1) they are relatively larger and more uniform in size than other scales, 2) they are less frequently distorted, and contain the most clearly defined annual rings 3) they grow at a reasonable rate 4) they appear to be formed during a relatively short period of time (Paul, 1968). Some scales are lost and replaced by others that have very large growth increments and no concentric rings in the centre of the scale. It was usually possible to exclude replacement scales as they were able to be identified macroscopically.

Scale aging works well with species that have large regular scales and Jones (1980) used scales for aging *N. celidotus*. However, Barrett (1995a) discounted scales for aging because the major growth checks were far too numerous and irregular in spacing to be annual. Otoliths provide a more representative record of growth than scales (Wootton, 1990). Barrett (1995a) found growth rings in sagittal otoliths were produced annually. The sagitta otoliths were removed by making a lateral cut at the dorsal base of the skull, then cutting horizontally forward breaking the skull open. The otoliths were removed and stored in 100% alcohol. Otoliths have an alternating sequence of opaque and translucent concentric zones. Ideally one opaque and one translucent zone represent one year's growth (Wootton, 1990). To validate the accuracy of aging by scales selected otoliths were examined and compared for estimated age. A selection of otoliths were kindly sectioned by Prof. J. H. Choat (James Cook University).

Scales were viewed under a stereo-microscope with reflected light off a black background and were read twice, independently, to check the validity of results. Age was defined as the number of completed years, with the final margin being counted as a year. It is acknowledged that scale reading is subjective and various workers can get different results. The subjectivity of scale reading was demonstrated by Mann & Steinmetz (1985) who had six scientists examine scales from known age Rudd, *Scardinus erythrophthalmus*. Five out of the six achieved less than 50% success, mainly due to misinterpretation of true or

false annuli and overlooking the first annuli. In the present study it was difficult to get non-replacement scales from the large specimens.

To validate scale aging the marginal increment, the distance from the last annulus to the scale edge, was measured with electronic calipers (Mitutoyo, Model CD-6 BS). This provides a measure of the relative amount of growth that had occurred since the last annulus was formed. Evidence for the annual formation of annuli was obtained by examining the marginal increments of the scales of fish between 190 - 220 grams throughout the year. This size class was selected as they represented the smallest size class that had at least three fish per month. It is acknowledged that marginal increment analysis is one of the weaker forms of validation (Gillanders, 1995b).

3.3 RESULTS

3.3.1 RELATIONSHIP BETWEEN COLOUR PHASE, SIZE AND SEX

The size frequency distribution of the sampled *Notolabrus fucicola* shows both sexes were distributed throughout the size range of 81 - 400 mm (Figure 3.1). There was no significant difference between male and female standard length ($p = 0.85$) or weight ($p = 0.21$). The presence of small and large males suggests this species is diandric.

N. fucicola does not appear to be sexually dichromatic as both sexes were found in both colour phases (Figure 3.2). However, there is an obvious relationship between size and colouration. There is a shift from IP in the smaller size classes to TP at larger sizes. This transition occurs over a large size range from 200 - 300 mm. Six percent of females and 8% of males were transitional in colour (Table 3.3). There were no TP fish below ^{190 180}170 mm. Some very large IP *N. fucicola* (350 mm) were observed during transects. There is no graph showing IP, TP and transitional fish for males and females across size classes, as both sexes followed an identical pattern as in Figure 3.2.

There was a bias towards females captured in the study. Of the 453 *N. fucicola* sampled 281 were females and 172 were males. This is an overall female to male ratio of 1.6: 1. The ratios of males to females changed from the IP to the TP colour phases. The percentage of male^s increased from 39% in the IP to 56% in the TP. The percentage of females decreased from 56% in the IP to 38% in the TP (Table 3.3).

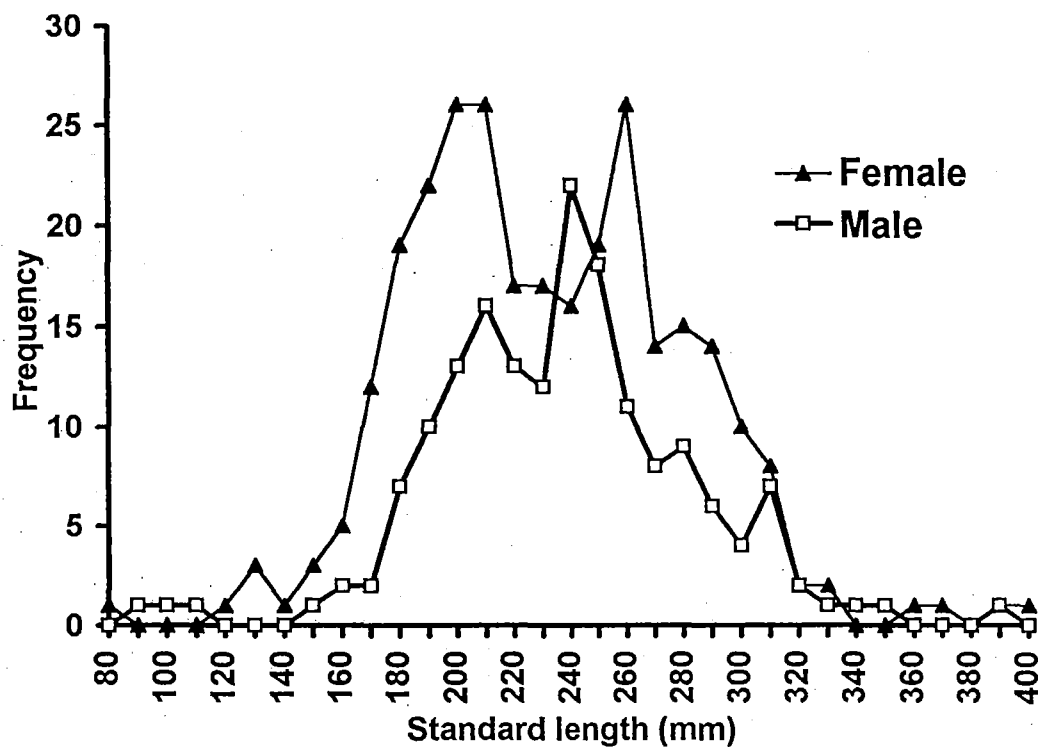


Figure 3.1 Size frequency distribution of male ($n = 172$) and female ($n = 281$) *Notolabrus fucicola* from samples collected around Kaikoura from Dec 1996 to Feb 1998.

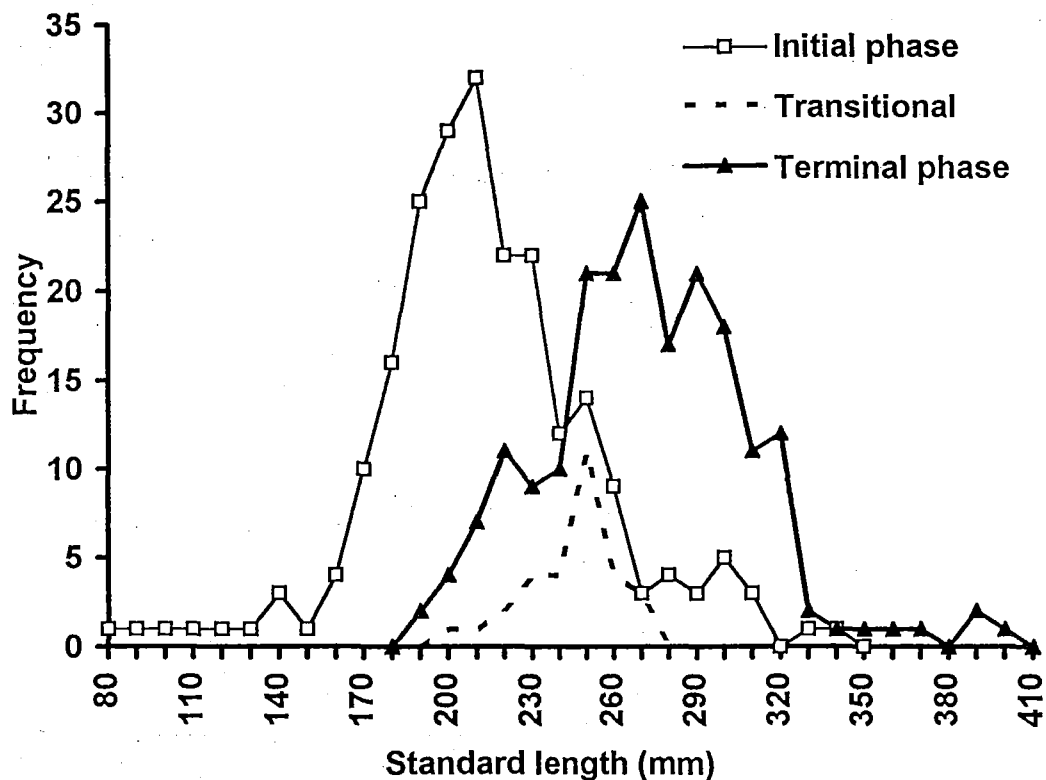


Figure 3.2 Size frequency distribution of initial ($n = 224$), transitional ($n = 30$) and terminal phase ($n = 199$) *Notolabrus fucicola* from samples collected around Kaikoura from Dec 1996 to Feb 1998.

Table 3.3 Number and percentage (in brackets) of male and female *Notolabrus fucicola* in each colour phase (initial, transitional and terminal) from examination of gonads from fish sampled around Kaikoura from Dec 1996 to Feb 1998 (n = 453).

	Colour Phase			
	Initial	Trans.	Terminal	Total
Female	157 (56%)	16 (65%)	108 (38%)	281
Male	67 (39%)	14 (8%)	91 (53%)	172

3.3.2 REPRODUCTIVE SEASONALITY

The annual seasonal patterns of breeding were examined for *Notolabrus fucicola*. For both males and females there was a marked increase in GSI values from July to December (Figure 3.3). Males and females followed similar trends in GSI values, but males peaked slightly before females in August, and again in December 1997. A peak also occurred during the previous December, with high GSI values recorded for both sexes. Both sexes appeared to peak in from August to October. The GSI declined to low levels by the end of January in both years and continued until June. There was a significant interaction between sex and month (Table 3.4) further indicating the seasonal variations in the reproductive cycle. There was no significant difference in the GSI values of males and females ($p = 0.556$) (Table 3.4).

An interesting pattern emerges when IP and TP males and females are compared. IP males had an initial peak early in the spawning season (July) but dropped dramatically after this month and remained low for the rest of the breeding period. TP males peaked in August and remained at a high level for the remainder of the breeding season (Figure 3.4a). This may indicate that IP males concentrate their spawning activity early in the spawning season.

Table 3.4 Analysis of variance on the gonosomatic index (GSI) of male and female *Nololabrus fucicola* over time and between sexes.

Source of variation	df	SS	MS	F-ratio	p-value
Months	14	296.56	21.18	16.37	0.000
Sex	1	0.45	0.45	0.35	0.556
Months x Sex	14	47.68	3.41	2.63	0.001
Residual	423	547.47	1.29		
Total	452				

Females of both colour phases followed a similar pattern throughout the breeding season with a peak in September for TP females and a peak in October for IP females (Figure 3.4b).

Weak evidence for an endogenous basis to the reproductive cycle in *N. fucicola* comes from a 335 mm female held in an aquarium for 18 months with no interactions with conspecifics. This fish had huge gravid ovaries with a massive GSI of 7.2 in August. This timing corresponded with peaks in the natural reproductive cycle.

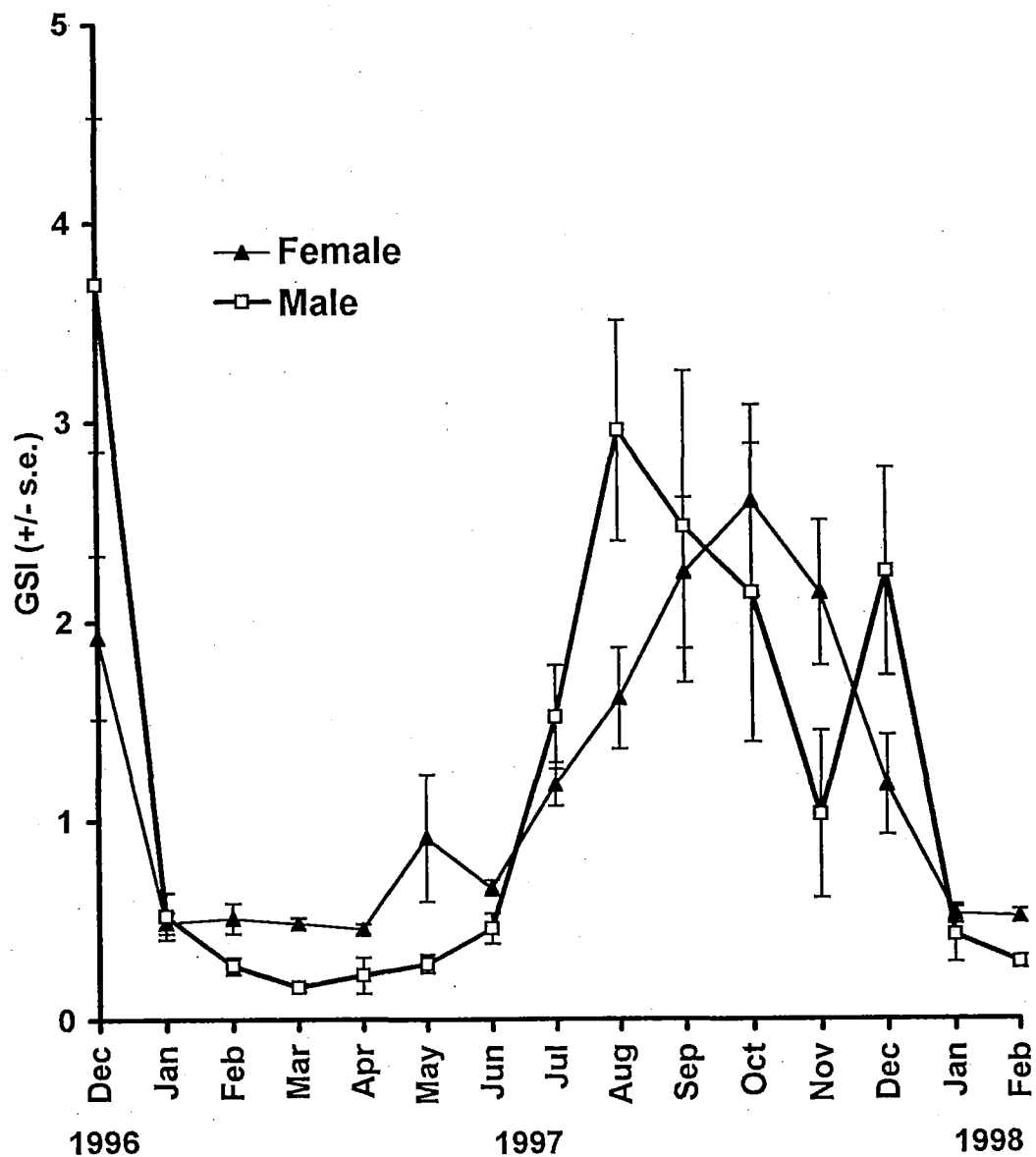


Figure 3.3 Mean monthly gonosomatic index (\pm s.e.) of male and female *Notolabrus fucicola* sampled around Kaikoura from Dec 1996 to Feb 1998.

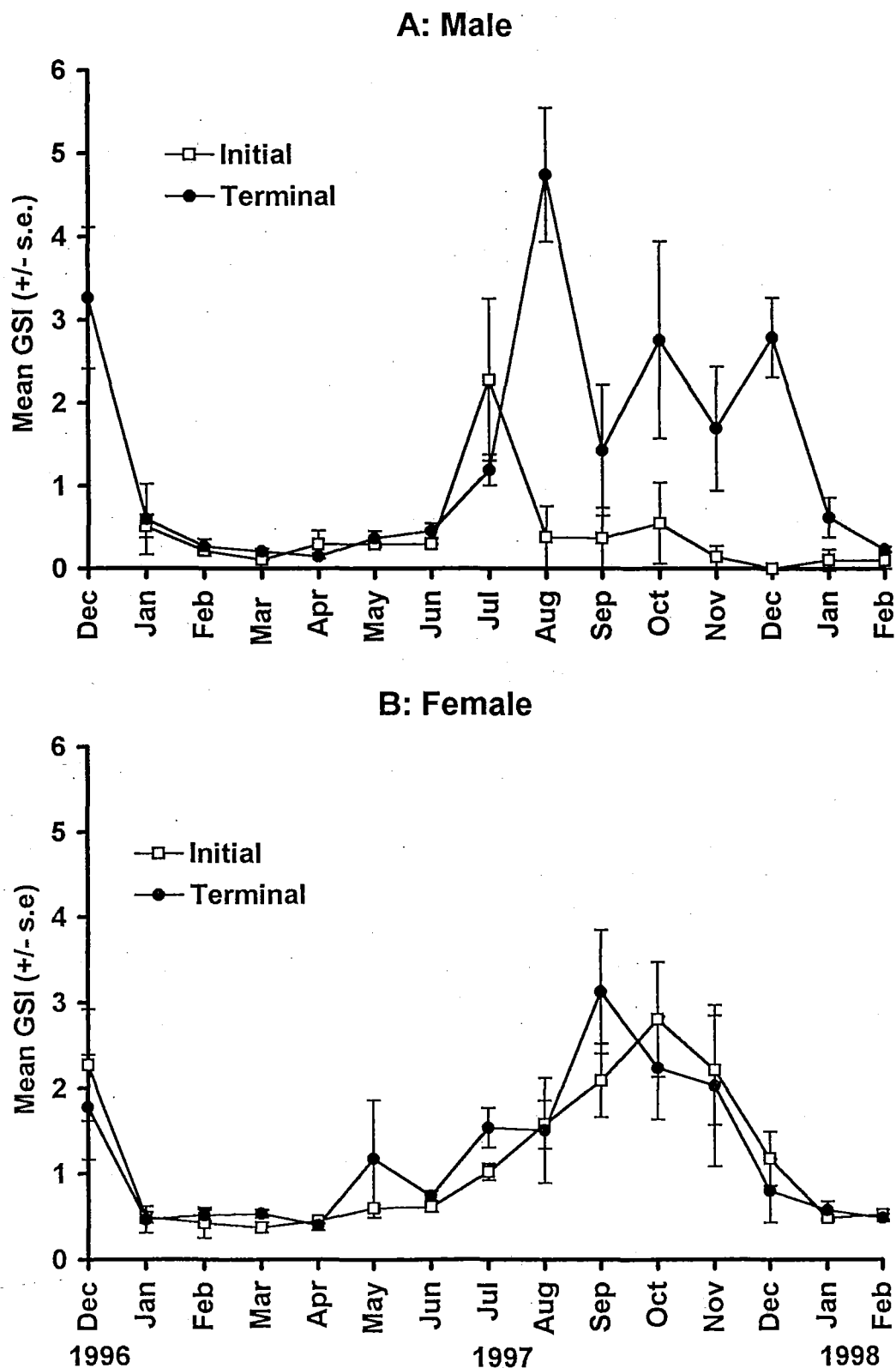


Figure 3.4 Mean monthly gonosomatic index (\pm s.e.) of initial and terminal phase male (A) and female (B) *Notolabrus fucicola* sampled around the Kaikoura Peninsula from Dec 1996 to Feb 1998.

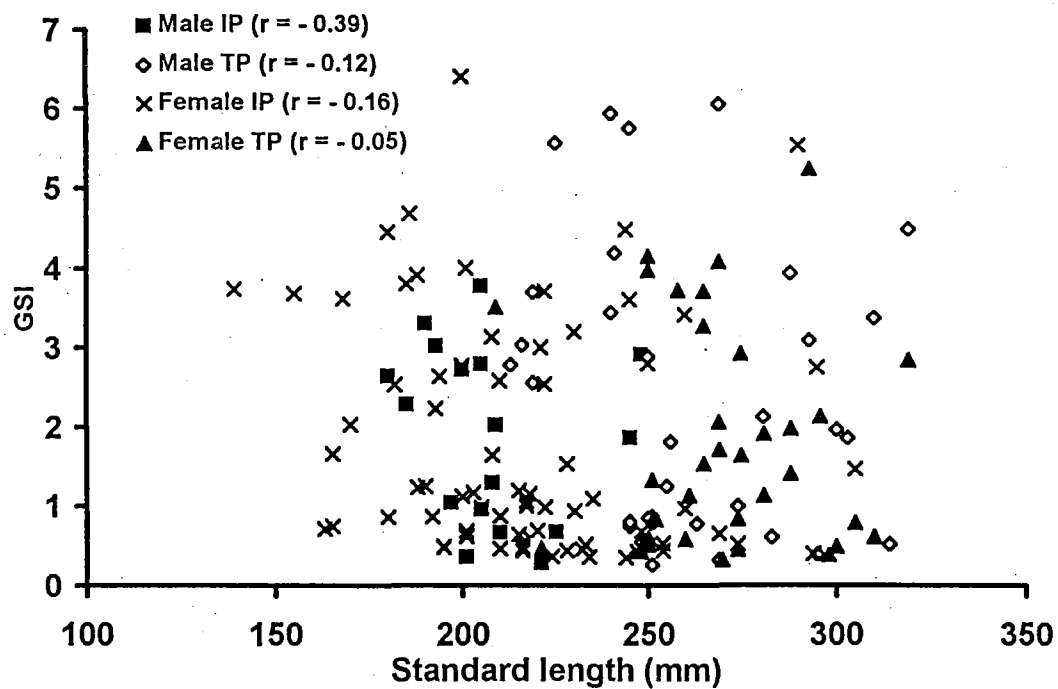


Figure 3.5 Scattergram showing the gonosomatic index versus standard length (mm) of initial and terminal phase male and female *Notolabrus fucicola* over the spawning period, July to December, 1997. Correlations given for each class.

There was no relationship between GSI values and the standard length of females and TP males (Figure 3.5). There is a negligible negative linear association between standard length and GSI for IP males ($r = -0.39$). The strong correlation between male sexual identity and relative gonad size for many other labrids was not evident for *N. fucicola*.

3.3.3 HISTOLOGY

The histological stages of *Notolabrus fucicola* gonads agreed with those described for other species (e.g. Bentivegna & Bendetto, 1989; Takashima & Hibiya, 1995). Histological staging showed seasonal changes in the gametogenic stages that coincided with the GSI cycle.

Gonads collected in December and January indicated that spawning had occurred for all fish examined. After spawning the ovary was relatively empty and contained mainly primary oocytes and atretic oocytes (Plate 3.1). Oocytes in any stage of vitellogenesis were rare in fish collected from February to May indicating spawning had ceased. These fish were in the resting phase, all containing primary or pre-vitellogenic oocytes and having a thickened gonad wall (Plate 3.2). Females collected from June to December generally had developing ovaries with eggs in several stages of vitellogenesis. For example, a female collected in July was undergoing stage one vitellogenesis (Plate 3.3). The oocytes are larger than in Plate 3.2 and the oocytes contain small lipid droplets. The chorion appears between the cytoplasm and follicle cells. Note that the nucleus has now become a germinal vesicle. Slightly different stages of development were found in mature females collected in December (Plate 3.4). Oocytes in this gonad have lipid droplets and large yolk vesicles. In Plate 3.5 these lipid droplets have coalesced into a large droplet and the germinal vesicle has begun its migration towards the periphery of the cell. This germinal vesicle migration is the final stage in maturation. Post-ovulatory follicles and atretic oocytes are present in Plate 3.5 suggesting spawning has occurred at least once already.

A lack of spermatogenic activity was observed in January and February with lucanae and primary spermatocytes predominated. Melano-macrophage centres (brown bodies) were present early in this period indicating spawning had ceased (Plate 3.6). This is a pre-reproductive phase where most semiferous lobules contained only cysts of spermatocytes. Larger

spermatocytes were observed from March to June (Plate 3.7 and 3.8). From July to November all phases of spermatogenesis were present but there was a decrease in the number of spermatogonia and spermatocytes and an increase in the number of spermatids and spermatozoa (Plate 3.9). A mature male collected in December shows the proliferation of spermatozoa into the sperm duct on the right (Plate 3.10). The peripheral location of this sperm duct suggests this is a secondary male gonad. This is typical of secondary males where the vas deferens surrounds the old oviduct (Warner, 1975b).

There was little evidence of post-maturational sex change or transitional gonads in any examined sections. However, a residual ovarian lumen was found in an immature small male (111 mm) (Plate 3.11), that suggest^s pre-maturational sex change. However, in most sections a distinct lumen was not found. This lumen may be difficult to identify in mature *N. fucicola* as testes have usually ruptured and evaginated or the lamellae had fused (Hourigan & Kelley, 1985). Although the gonad in Plate 3.11 could be viewed as a female, this gonad displays the typical male gonad shape.

The size at maturity for both males and females occurs over a size range from 94 to 133 mm, or between two and three years old. The smallest female, 81 mm, appeared to have developing oocytes as a few pre-vitellogenic oocytes were present (Plate 3.12). A 133 mm female was mature. Interestingly, the smallest male collected, 94 mm, had mature testes but ^aslightly larger male, 111 mm, was immature.

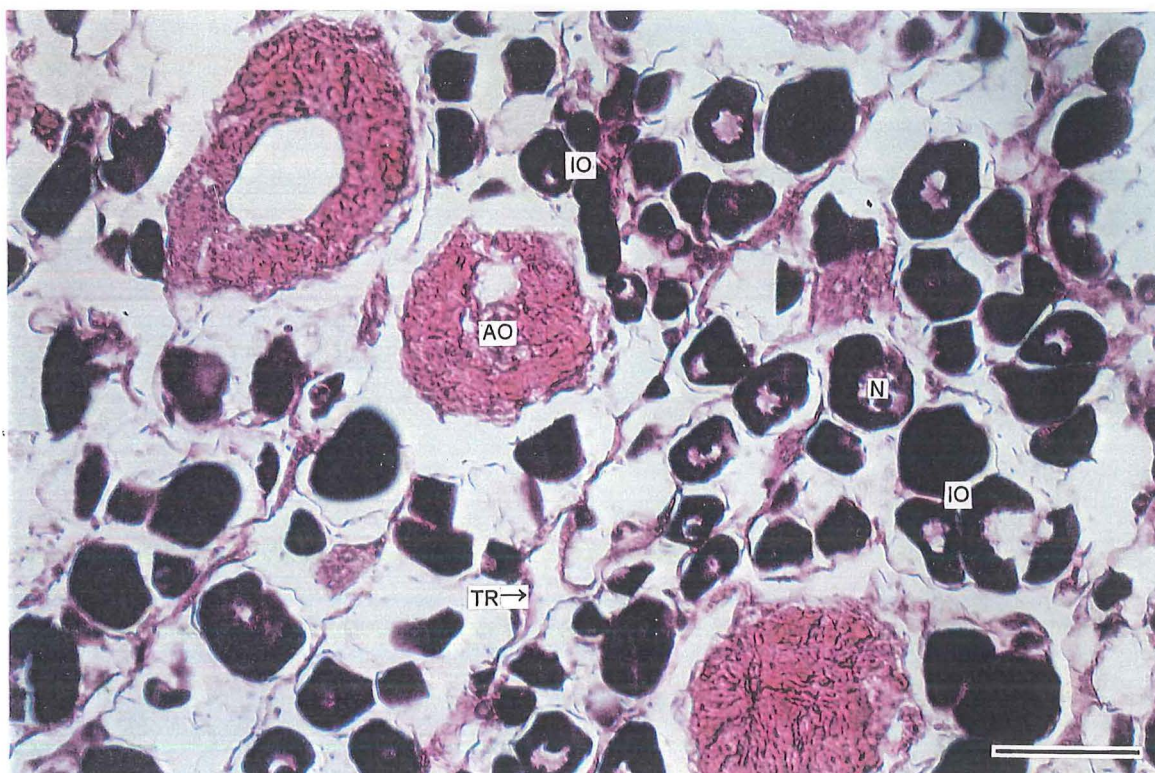


Plate 3.1 Post spawned female collected in January with characteristic atretic oocytes (AO) and immature (pre-vitellogenic) oocytes (IO). Note the nucleus (N) in the chromatin nucleolus oocytes and the trabeculae (TR). Scale bar is 0.1 mm.

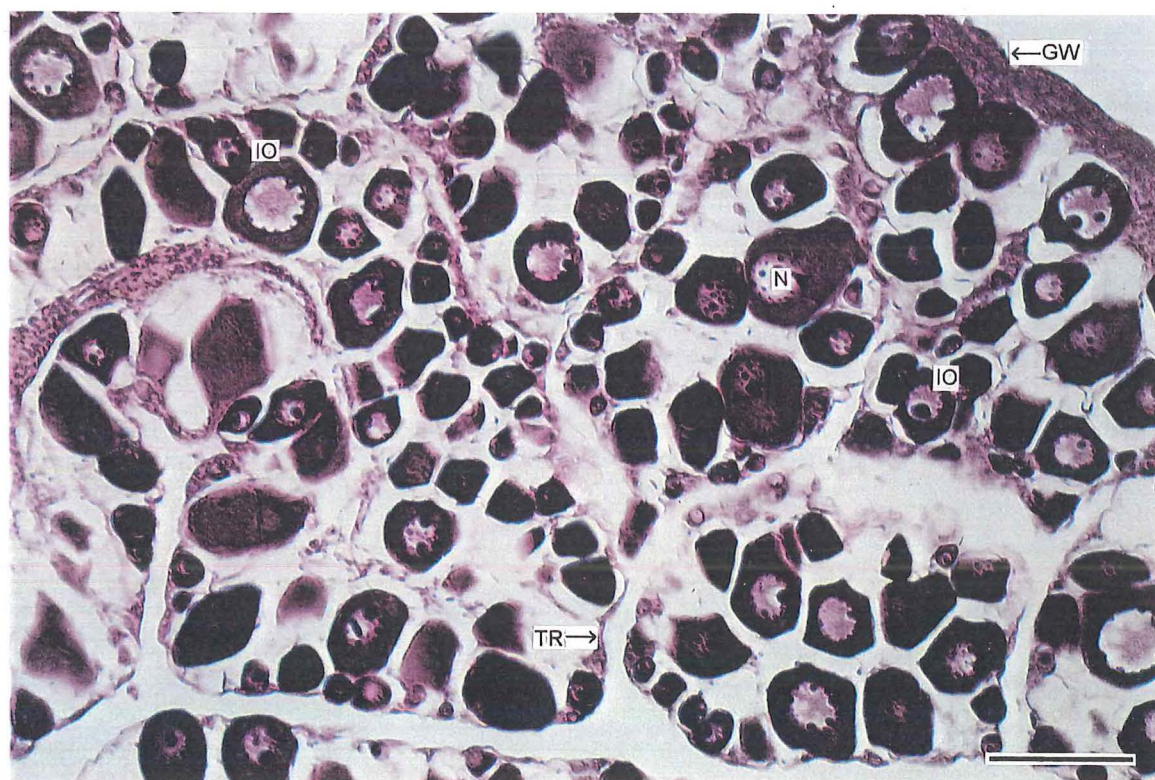


Plate 3.2 A resting ovary from a female collected in February with a dominance of immature (pre-vitellogenic) oocytes (IO) and a thickened gonad wall (GW). Note the nucleolus in the nucleus (N) and the trabeculae (TR). Scale bar is 0.1 mm.

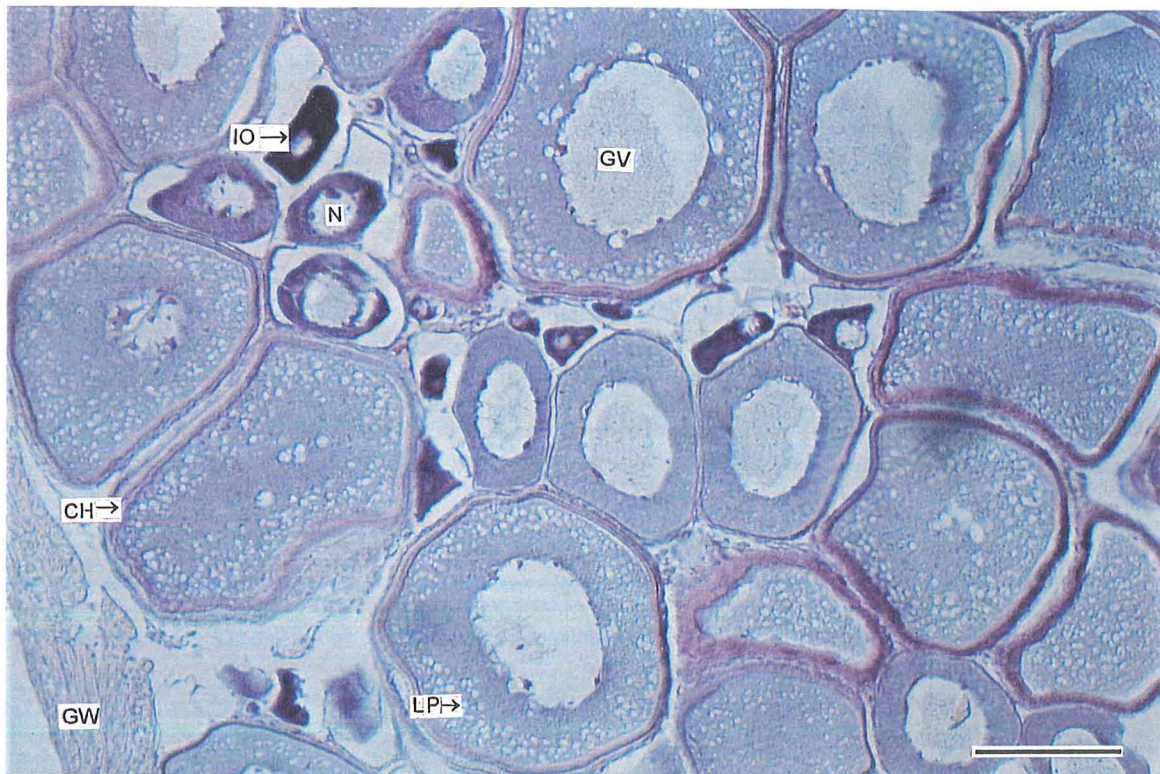


Plate 3.3 Female undergoing stage one vitellogenesis collected in July. Oocytes have increased in size and lipid droplets (LP) have appeared. The germinal vesicle (GV) and the chorion (CH) have appeared. Note the gonad wall (GW), nucleus (N) and immature oocytes (IO). Scale bar is 0.05 mm.

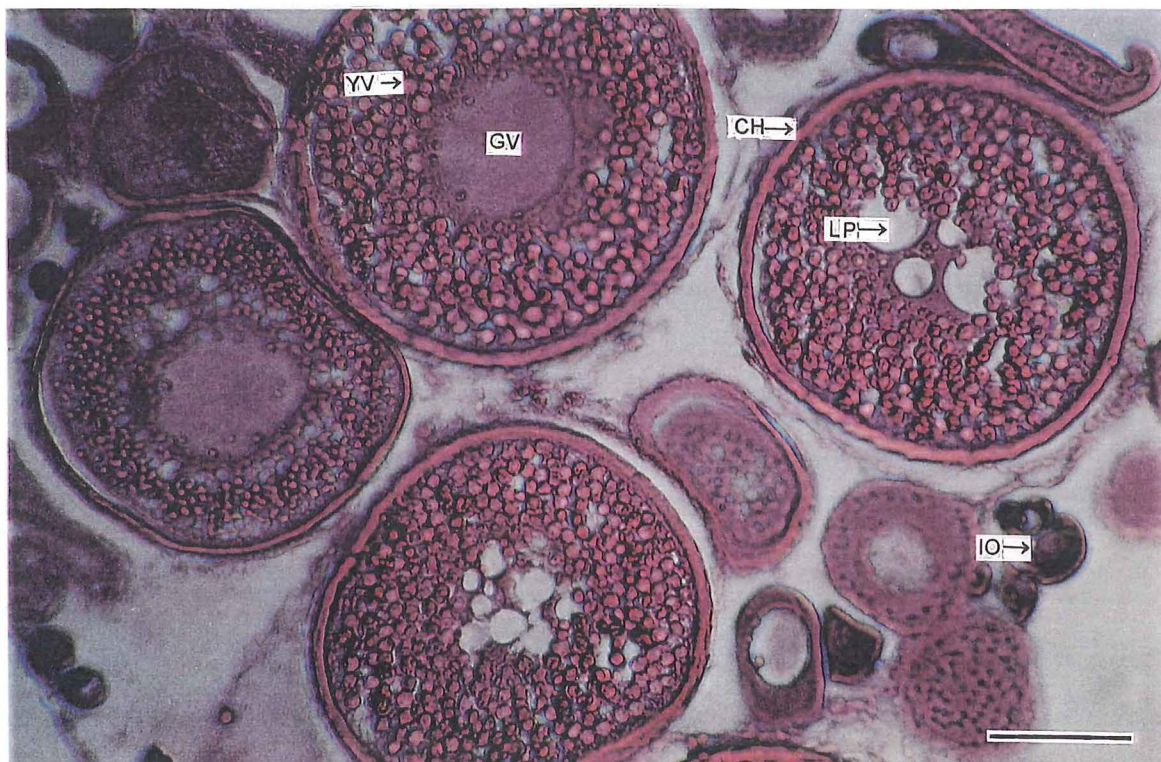


Plate 3.4 Mature female collected in December. The germinal vesicle (GV) is at the centre of the oocyte and is surrounded by yolk vesicles (YV) and lipid droplets (LP). Note the presence of immature oocytes (IO) and a chorion (CH). Scale bar is 0.05 mm.

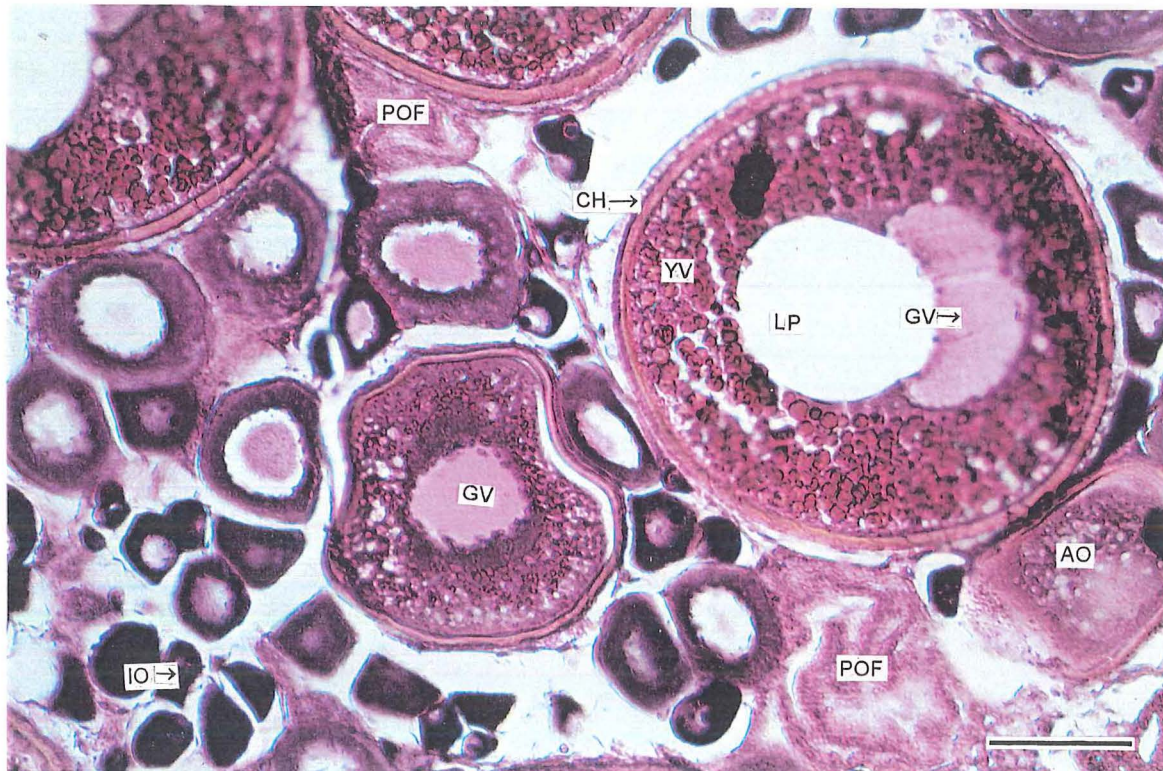


Plate 3.5 Late maturing female collected in December with post-ovulatory follicles (POF) and atretic oocytes (AO). Note the lipid droplets (LP) have coalesced into a large droplet and the germinal vesicle is migrating towards the periphery. Also note the presence of immature oocytes (IO) and the chorion (CH). Scale bar is 0.05 mm.

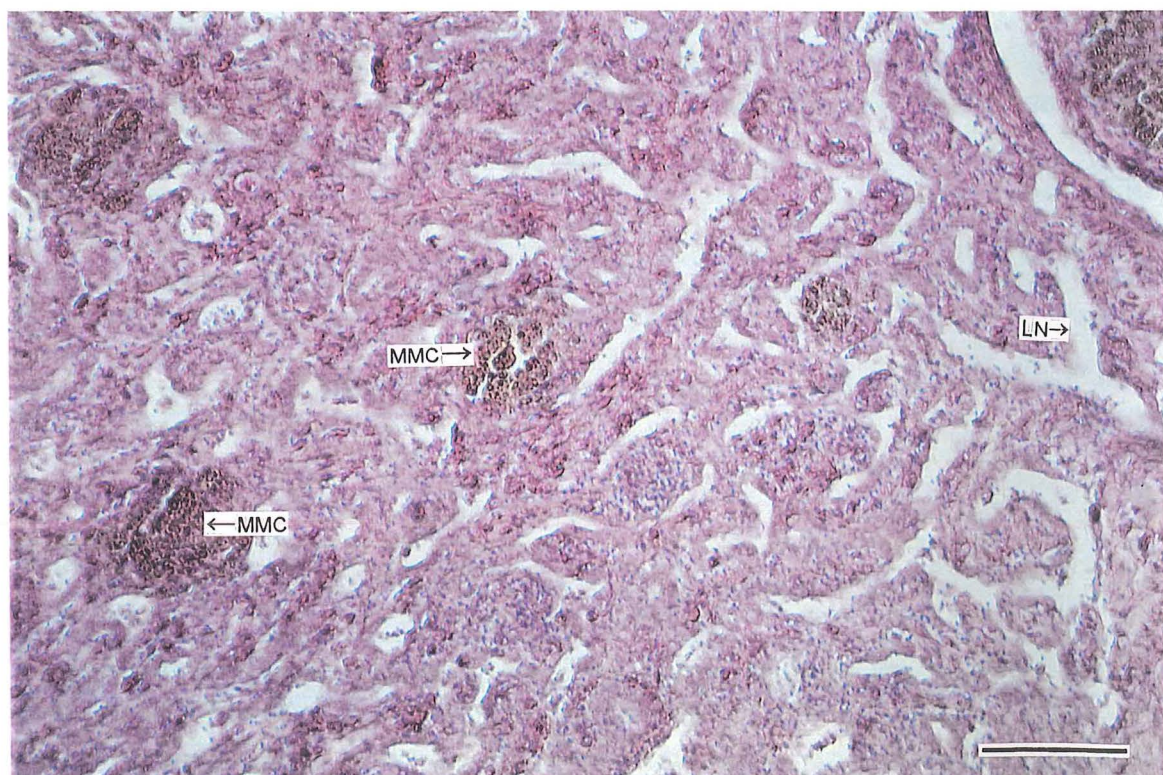


Plate 3.6 Post spawned male collected in February. Note the presence of melano-macrophage centres (MMC) and lucinae (LN). Scale bar is 0.05 mm.

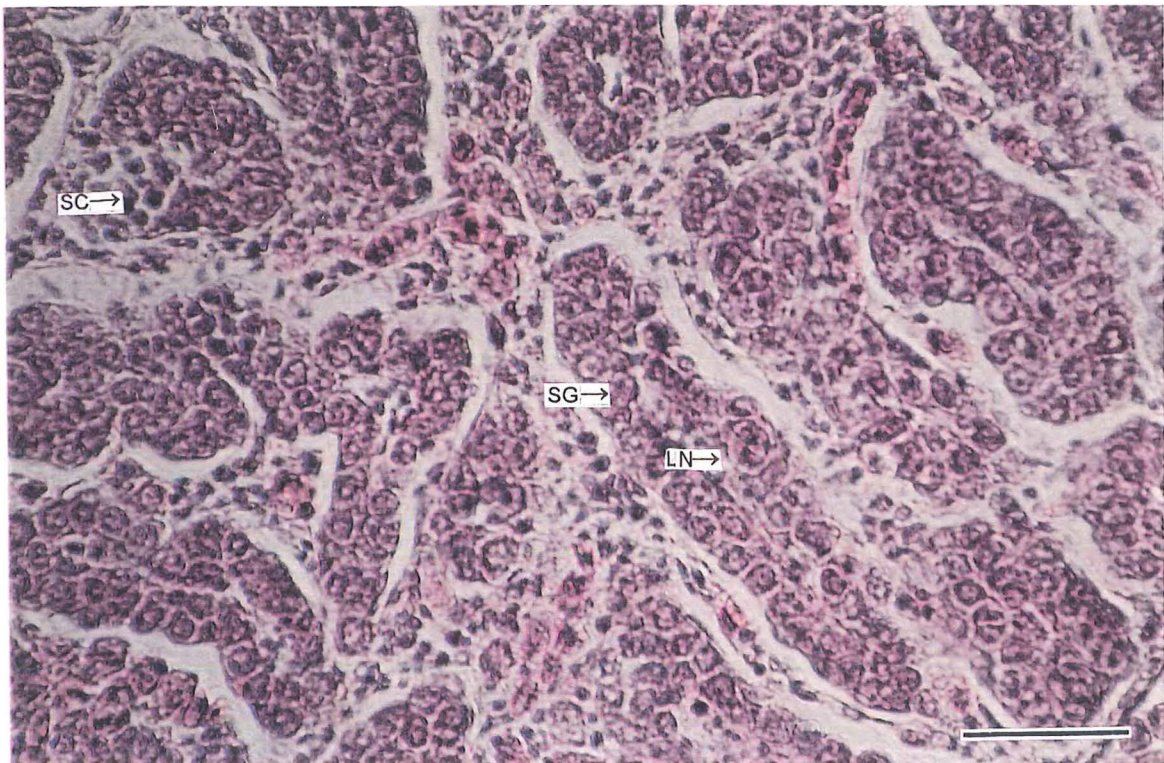


Plate 3.7 Male collected in March showing the onset of spermatogenic development with the presence of spermatogonia (SG) and spermatocytes (SC) around the periphery of the lucanae (LN). Scale bar is 0.03 mm.

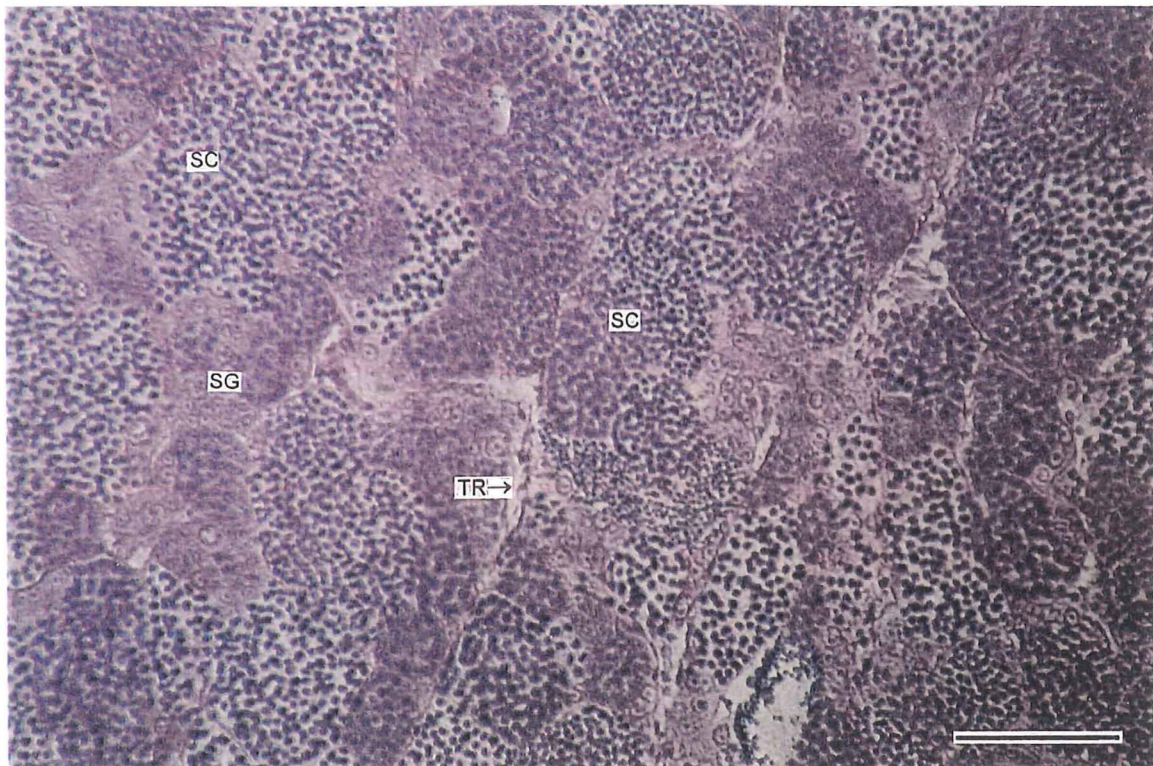


Plate 3.8 Developing male collected in April. Note the presence of spermatogonia (SG), the proliferation of spermatocytes (SC) and the trabeculae (TR). Scale bar is 0.03 mm.

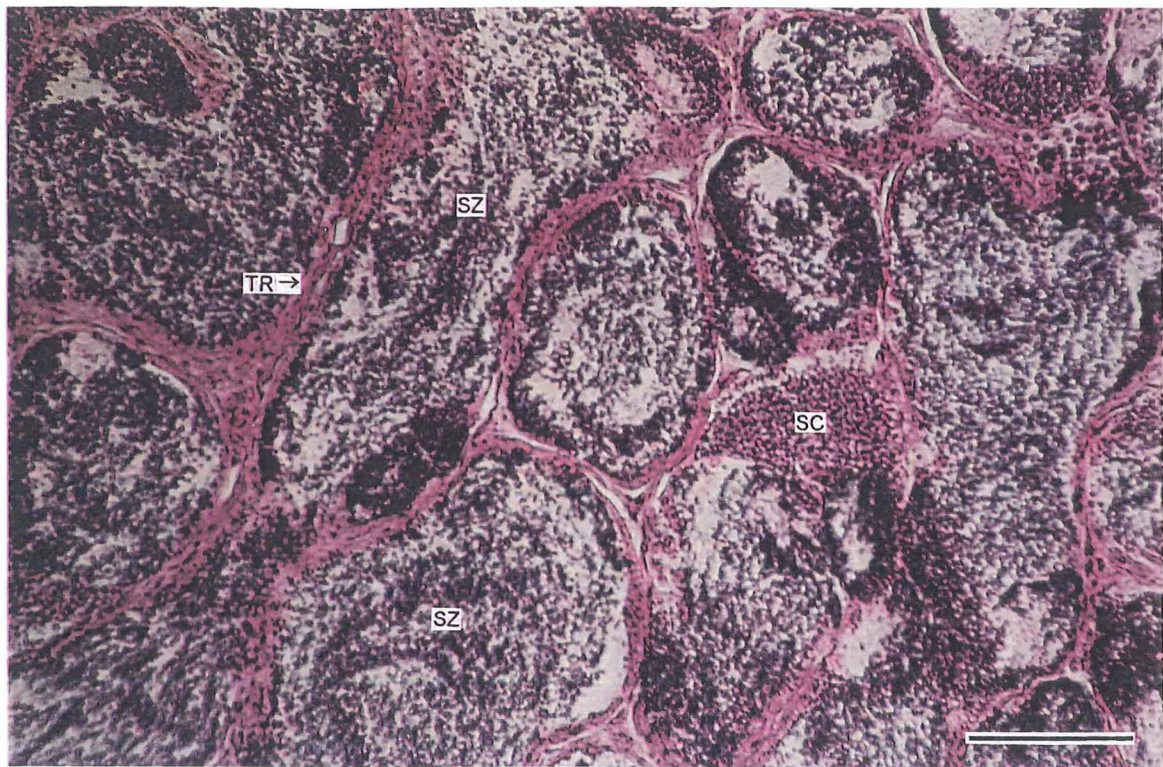


Plate 3.9 Mature male collected in August with increased numbers of spermatozoa (SZ). Note the presence of a small number of spermatocytes (SC) and the trabeculae (TR). Scale Bar is 0.03 mm.

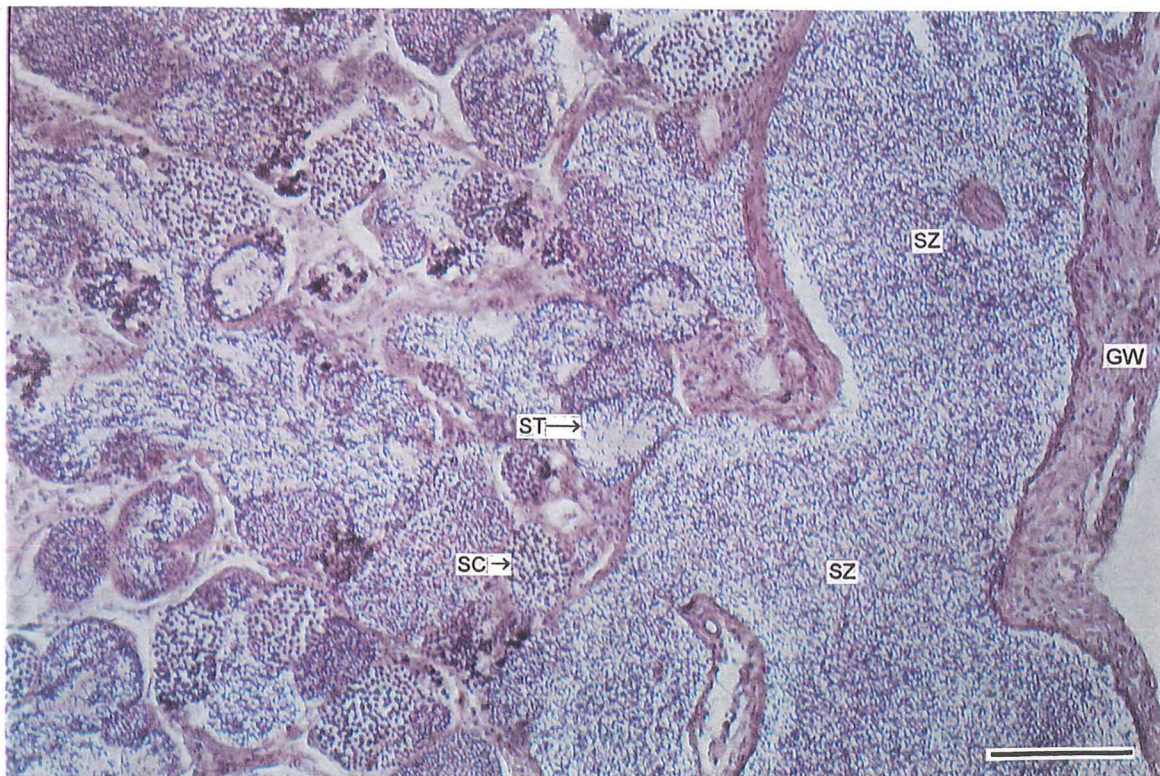


Plate 3.10 Mature male collected in December showing several stages of spermatogenesis. Note the sperm duct on the right full of spermatozoa (SZ) and the thick gonad wall (GW). Also present in smaller amounts are spermatids (ST) and spermatocytes (SC). Scale bar is 0.05 mm.



Plate 3.11 Immature male (111 mm SL) with a residual ovarian lumen (RL). Note the high amount of connective tissue (CT). Scale bar is 0.1 mm.

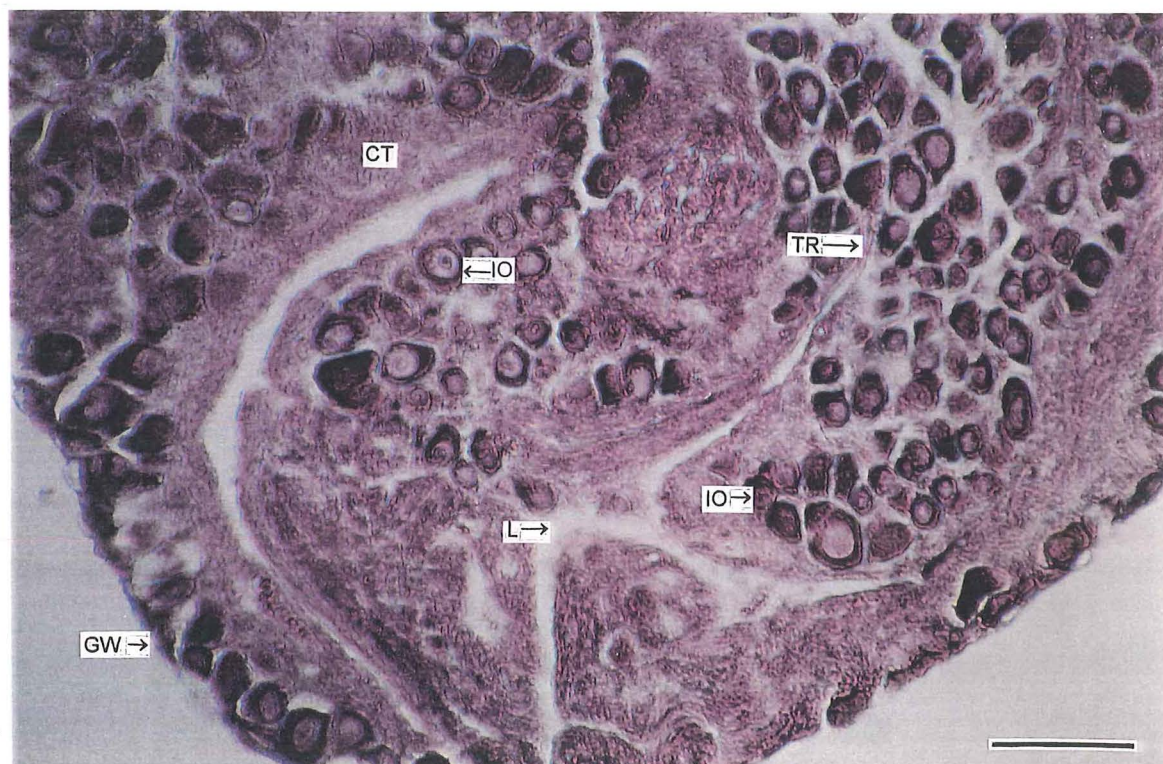


Plate 3.12 Ovary collected from an immature female (81 mm SL). Note the high amount of connective tissue (CT), the development of immature oocytes (IO) and the ovarian lumen (L). Also note the trabeculae (TR) and the thin gonad wall (GW). Scale bar is 0.1 mm.

3.3.4 AGE AND GROWTH

Notolabrus fucicola are ~~a~~ long-lived, reaching at least 25 years (350 mm) with an average age of 9 years (Figure 3.6). A few fish larger than 350 mm were captured but the scales and otoliths could not be read. The scales were either replacement or blurred at the margins and the otoliths could not be read, because of confusing rings. Scales were read independently twice. Although this involves a subjective interpretation of the annuli, both checks yielded similar results ($r = 0.82$).

Scale data followed a linear pattern until the twelfth year and then became more erratic. Scale and otolith results followed different linear trendlines (Figure 3.6). Scales tended to overestimated ages compared to otoliths, which is unusual as most authors found that scales underestimate age (Paul, 1986; Beamish and McFarlane, 1987; Carlander, 1987). However, it is difficult to make detailed comparisons between scales and otoliths as only 32 otoliths were examined ^{because} ~~as~~ they required special preparation, not possible with the facilities in Kaikoura.

N. fucicola appears to grow rapidly over the first two to three years reaching 100 mm in length. There appears to be a slowing down of growth after this initial growth spurt and it seems that *N. fucicola* continues to grow steadily throughout their life. From scale data, it appears the growth of very large fish slows. However, this should be treated with caution as only three large fish were aged and scales are notoriously bad at accurately aging older fish (Beamish & McFarlane, 1987). Analysis of variance found there was no difference in the growth rate of male and female *N. fucicola* ($p = 0.244$). The three oldest fish were females (Figure 3.7).

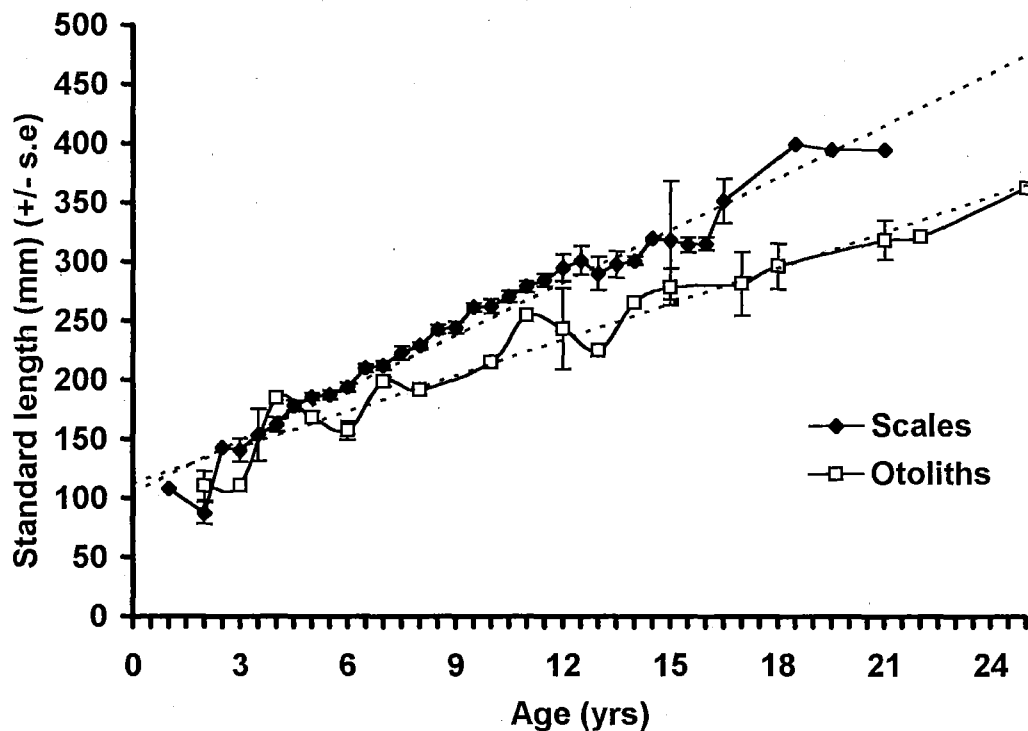


Figure 3.6 Standard length (mm) versus age (+/- s.e.) of *Notolabrus fucicola* using scales (n = 452) and otoliths (n = 31). Dotted lines are linear trendlines. When no bars are present, the value is based on one or two fish.

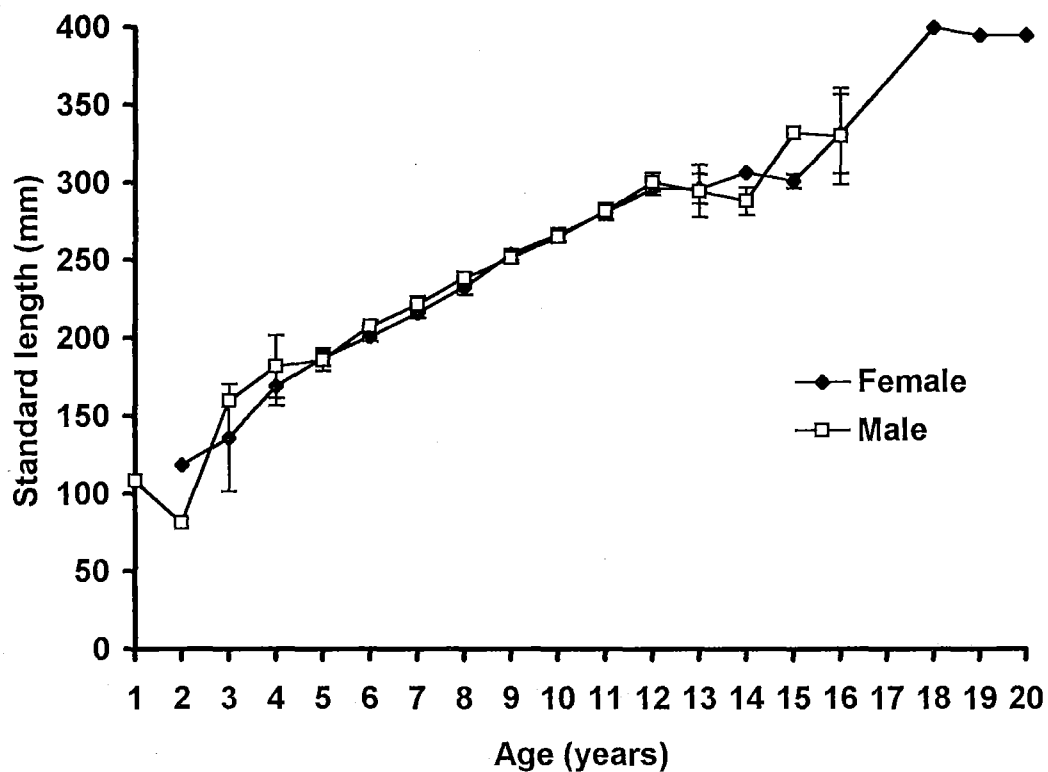


Figure 3.7 Relationship between standard length and age (+/- s.e.) for male and female *Notolabrus fucicola* (from scales) (n = 452).

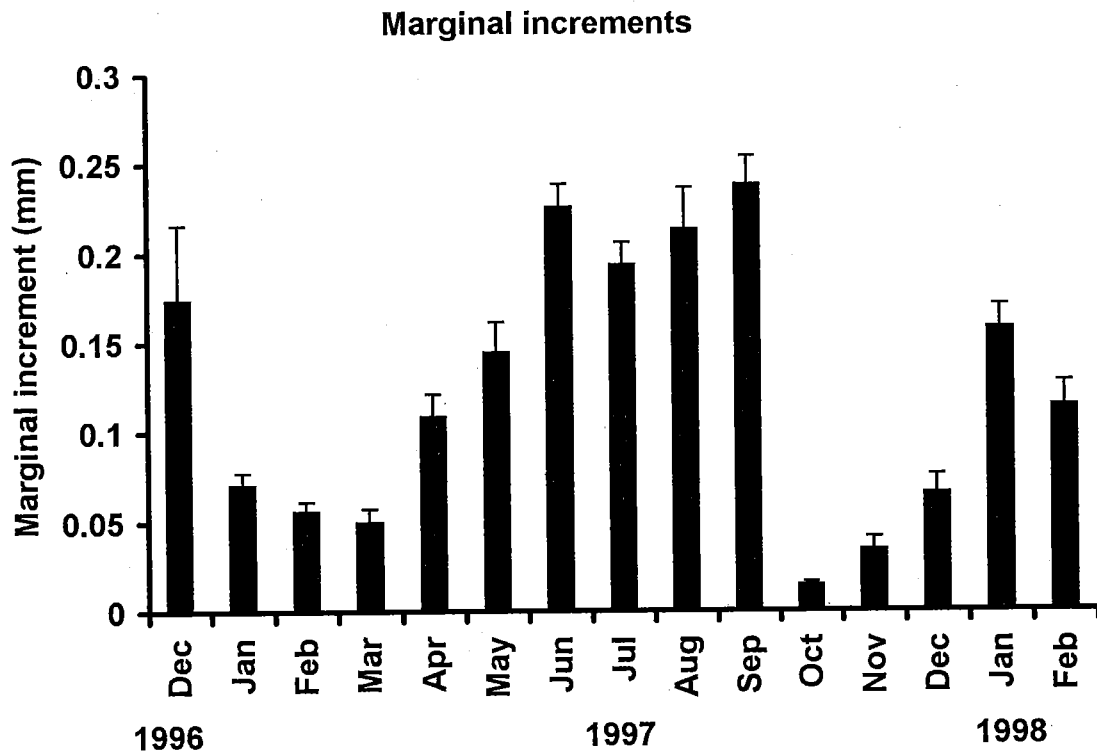


Figure 3.10 Marginal increment analysis (+ s.e.) of scales from 200-210 mm SL *Notolabrus fucicola* sampled from Dec 1996 to Feb 1998.

Marginal increment analysis, from fish weighting between 190 - 220 grams, suggests that an annulus may be laid down in October (Figure 3.8). This is not conclusive because for the first four months there was no obvious increase in increment width.

3.4 DISCUSSION

3.4.1 RELATIONSHIP BETWEEN COLOUR PHASE, SIZE AND SEX

Notolabrus fucicola males and females were distributed throughout similar size ranges. Russell (1988) and Barrett (1995a) also noted that the sizes of males and female *N. fucicola* overlap broadly. This is unusual for labrids as females typically dominate the smaller size classes and males occur almost exclusively in the larger size classes. The fact that both sexes were represented among all size classes suggests that *N. fucicola* may not be hermaphroditic. For example, Robertson & Justines (1982) found that Caribbean gobies that had males and females distributed throughout the size range ^{were} ~~to be~~ gonochorists. However, even sex distributions are not definitive indicators of gonochorism. For example, the gobiid *Coryphopterus personatus* is a protogynous hermaphrodite yet the size distributions overlap almost completely. Some males develop directly from a functional female phase while others pass through an immature female-like phase and then become males at small sizes (Sadovy & Shapiro, 1987). The presence of both small and large males suggests that *N. fucicola* is diandric. However, because all males appear to be derived the same way (i.e. before maturation), this species is defined as monandric.

Many labrids exhibit a distinct demarcation between colouration and sex. Although *N. fucicola* exhibits two colour phases, there was no marked sexual dichromatism meaning this species is monochromatic. The presence of males and females in both colour phases is unusual as most labrid studies predict that females should dominate the IP and males dominate the TP. Initial phase fish dominate the smaller size classes with a changeover to the TP occurring between approximately 200 to 300 mm. Thompson (1981) reported IP fish average between 150 -200 mm whereas TP fish are 150 - 300 mm in length. The significance of this colour change is unknown, but is likely to be a result of habitat change. The colour pattern of IP fish may camouflage them in seaweed, whereas the darker colouration of TP fish may help them blend with rocks or

make them more difficult to see in the water column. Additionally, the yellow bands on TP fish may break up their shape, so movement through seaweed may cause them to blend together in the eyes of a predator (flicker fusion) (Moyle & Cech, 1982).

The percentage of IP males in *N. fucicola*, 39%, agrees with other authors (Doak, 1978; Thompson, 1981; Francis, 1988) who found similarly high proportions of IP males in this species. Gonochorists tend to have a higher proportion of males in the initial phase. For example, the percentage of males in initial phase *Symphodus ocellatus* was 48% (Bentivegna & Bendetto, 1989). The high percentage of IP males is likely to be due to the social structure of the population (discussed below). There was an approximately even proportion of males and females in the TP.

Protogynous species tend to have a sex ratio biased towards females. The greater abundance of females arises due to differentially high mating success of territorial males (Warner & Hoffman, 1980a). For example, *A. viridis* ratios ranged from a female bias of 4: 1 to 62: 1 at different sites (Gillanders, 1995b). On the other hand, gonochoristic species tend to have an approximately equal ratio of males to females. In my study the ratio of males to females was slightly higher than would be predicted for gonochoristic species at 1.6: 1. This is also slightly higher than the 1: 1 ratio that Barrett (1995a) found for this species. However, while an equal sex ratio does indicate gonochorism it is not definite proof. For example, the protogynous labrid, *Semicossyphus pulcher*, has a ratio of females to male between 3: 1 and 0.8: 1 (Cowen, 1990).

3.4.2 REPRODUCTIVE SEASONALITY

The spawning season of *Notolabrus fucicola*, as in most temperate labrids, occurs over a period of ^{? approximately} appropriately five months from July until December. This was evident in both the GSI and histological staging. Atretic oocytes and POF, found in late December and January, occur following spawning. All vitellogenic oocytes remaining in the ovary after spawning are invaded by granulosa cells, that phagocytose the oocyte remains (Dipper & Pullin, 1979). The observations in this study, plus those of Robertson (1973) in Otago, Doak (1972) in northern New Zealand and Barrett (1995a) in Tasmania indicate that spawning probably occurs at the same time over New Zealand and Australia. This is surprising as the breeding season of the related species, *N. celidotus* in Wellington was delayed approximately one month compared to that in northeastern New Zealand (Thompson, 1981), probably linked to water temperature differences. Robertson (1980) found eggs and larvae of *N. fucicola* in the plankton around Otago when the water temperature was at a minimum. An increase in the GSI of *N. fucicola* in this study occurred shortly after the shortest day and lowest water temperatures. The rationale for spawning when the water temperature is rising may be related to higher levels of primary production, a factor that could enhance the survival and growth of larval fishes.

The GSI of *N. fucicola* remained relatively high from August to December, and from June to December females displayed varying stages of vitellogenic oocytes. The five months of high GSI values of *N. fucicola* contrasts with *N. celidotus* for which the spawning activity was concentrated during the first two months of the spawning season (Jones & Thompson, 1980). However, *N. fucicola* males had highest GSI values early in the spawning season (July and August) which suggests they concentrate spawning activity early in the reproductive season. The GSI revealed an interesting pattern in regard to IP and TP male GSI values. IP males peaked slightly earlier than TP males but dropped back to pre-spawn baseline levels immediately after this peak. There are several theories to explain why this occurred: 1) IP males may begin

breeding activities early in the spawning season, and once they become recognised by territorial males find themselves unable to spawn. However, this idea differs from the suggestion of Gillanders (1995b) that larger fish may spawn earlier in the season ^{an} the smaller fish; 2) once larger males are ready to spawn smaller males may be excluded from pair spawning; 3) it is possible that IP males adjust their testes size in response to breeding opportunities. For example, large successful *N. celidotus* males had larger testes than unsuccessful ones, relative to body size, and 4) IP males may invest more energy into growth while small in order to gain increased benefit in reproduction while large (Warner, 1982). Also, energy may be diverted from reproduction to growth and other areas to enhance survival, for example, resistance to infection.

In several fish species, larger females ripen and spawn before smaller ones (Pottle & Green, 1977; Jones & Thompson, 1981). For example, *N. fucicola* from north-eastern New Zealand exhibited delayed spawning of small females (Jones & Ayling, unpublished data: cited in Jones & Thompson, 1981). This was not the case for *N. fucicola* in my study where both IP and TP females followed a similar GSI pattern.

3.4.2 REPRODUCTIVE BIOLOGY

Gonochorism and protogynous hermaphroditism are two distinct reproductive strategies found in the family Labridae (Dipper & Pullin, 1979). Although protogyny is the most common reproductive strategy in labrids, there are many examples of gonochoristic species, usually in the northern hemisphere (see Dipper & Pullin, 1979; Costello, 1991). My study confirmed through histological examination of 90 gonads that *Notolabrus fucicola* is a secondary gonochorist.

In monandric species the typical secondary testis structure reflects its ovarian origins with a lamellar configuration and the retention of the old ovarian lumen

(Dipper & Pullin, 1979; Nemptzov, 1985). The gonads of all individuals pass through an early ovarian stage before developing into a mature ovary or testis (Shapiro, 1987). In this system the sexes are genetically determined, with all males having secondary testes that have developed the male condition before maturation (Barrett, 1995a). In the present study very small testes had a residual ovarian lumen, indicative of secondary males. Barrett (1995a) also found that the testes of all males examined had a residual lumen, although it was difficult to recognise initially, as the testes had either split and evaginated or the lamellae had fused in mature specimens. A similar sexual system to *N. fucicola* was found in the North American temperate labrid *Oxyjulis californica* (Deiner, 1976: cited in Barrett, 1995a). For a detailed description of primary and secondary male gonad structure see Shapiro and Rasotto (1993).

Although there were no observed incidences of post-maturational sex change for *N. fucicola* in this study, there are reports that a small proportion of female *N. fucicola* are capable of changing sex at any time (Thompson, 1981; Jones, pers. com.). The significance of this is unknown but is likely to be influenced by social stimuli as there is no evidence for sex change on reaching a particular size or age. Females of this species may change sex in populations when female numbers begin to substantially outnumber males (Shapiro & Lubbock, 1980). Barrett (1995a) hypothesised that the mode of reproduction in the New Zealand population may differ from that observed in the Tasmanian population. He explained the lack of sex change in Tasmanian populations could be attributed to their physical isolation by distance (limiting gene flow).

N. fucicola does not fit the typical pattern for gonochorism where males have little or no opportunity to change sex. Usually, gonochoristic species live in a complex harem social structure or at relatively high population densities. Also, they tend to engage in prolonged courtship and mating rituals, and display parental care (Warner & Lejeune, 1985). *N. fucicola* do not fit these criteria as this species is not harem, does not appear to live at high population densities (approximately 2 - 6 per 150 m²) and does not display nesting behaviour or parental care. Additionally, the growth rate was not

significantly different, between the sexes, which contrasts with other gonochoristic species where males have a significantly higher growth rate (Dipper *et al.*, 1977). Moreover, *N. fucicola* are a large, long-lived species and sex change was suggested to be more likely to develop in this situation (Dipper & Pullin, 1979). Furthermore, pair spawning in a lekking system observed by Jones (pers. com.), are the circumstances in which protogyny would be expected to evolve.

The causes of gonochorism in *N. fucicola* are therefore uncertain but several theories suggest how gonochorism may have evolved in this species. Barrett (1995a) suggested that the lack of sex change in Tasmanian populations of *N. fucicola* was because the territorial behaviour typical of labrids would be difficult to maintain in shallow waters along the high energy coastlines of Tasmania. Without the social control that territorial behaviour enables, the proportion of IP males would be expected to increase, as predicted by Robertson and Choat (1974), or the average size of TP males would decrease due to lack of inhibition of sex change by dominant males. This hypothesis is difficult to apply to *N. fucicola* around Kaikoura as they exhibit definite territoriality.

An alternative hypothesis may be the lack of social control that occurs in populations with high densities. Labrids that live at high densities, such as *Thalassoma lucasanum*, have higher numbers of IP males which in turn lowers the mating efficiency of territorial terminal phase males (Warner, 1982). These populations are characterised by group spawning, in which larger males do not accrue disproportionately high mating success. This social system selects against sex change because sex changing individuals are favoured in situations where small males are excluded from breeding (Warner & Hoffman, 1980a; Warner, 1982). Warner & Hoffman (1980a) predicted that smaller males are able to gain some reproductive success because large TP males cannot effectively exclude them from spawning. Although the populations did not appear to be particularly dense, this seems to be the most likely hypothesis to account for the lack of sex change in *N. fucicola* around Kaikoura. A further

idea was suggested by Jones (pers. com.) where irregular recruitment may select against sex change. However, he admitted this idea was probably incongruous.

Various types of spawning behaviour have been reported in *N. fucicola*. For example, Barrett (pers. com.) reported mass spawning aggregations of *N. fucicola*, with numerous males (up to 20) chasing individual ripe females. They performed spawning maneuvers, released copious amounts of sperm, then the males moved onto the next female ready to spawn. Alternatively, Thompson (1981) and Jones (pers. com.) observed pair spawning in some sort of lekking system at Leigh. Differences in spawning strategies appear to arise because of differing population densities. High density populations engage in group spawning whereas low density populations engage in pair spawning (Warner & Robertson, 1978). In species that have a high proportion of IP males, such as *N. fucicola*, males tend to take part in group spawning and often have extremely large testes when ripe (Dipper & Pullin, 1979; Warner, 1982). Indeed, *N. fucicola* males have high GSI values that is characteristic of group spawners that need to produce large amounts of sperm in order to fertilise as many eggs as possible. Further evidence for group spawning comes from the lack of sexual dichromatism. It has been suggested that sexual dichromatism has developed in labrids in which males must compete for females during spawning periods. This is because the display of a distinctive, conspicuous colour pattern enhances the males ability to attract a mate (Robertson, 1981). *N. fucicola* has both TP males and females that suggests females do not select males

The strong correlation between male sexual identity and relative gonad size that exists for many other labrids was not evident for *N. fucicola*. Typically, testes of small IP males are markedly heavier than those of secondary males (Robertson & Choat, 1974). This is primarily because primary males engage in group spawning or streaking that demands large quantities of sperm to ensure mating success (Choat, 1969; Robertson & Choat, 1974; Shapiro *et al.*, 1994; Helfman *et al.*, 1997). For example, some bluegill sunfish, *Lepomis macrochirus*, guard nests and attract females, whereas others sneak into a

territory to join a spawning nest guarder. The GSI for territorial males are about 1% but for sneakers it is 4.5%. Reasoning for lower GSI for territorial males may be because they release fewer sperm (Shapiro & Rasotto, 1993; Macconato *et al.*, 1995; Warner *et al.*, 1995). Male IP *N. fucicola* showed the opposite trend of many labrids and had GSI values lower than TP males.

It does not appear fecundity increases with length for *N. fucicola*. There was no relationship between the standard length and the GSI of females during the breeding period with very small females having GSI values equivalent to very large females. This suggests that females invest a similar amount of energy into reproduction regardless of size. Additionally, both initial and TP females followed a similar GSI pattern. This contrasts with other authors who found *N. celidotus*, *N. fucicola*, *P. miles*, and *Suezichthys* species exhibit size/age specific differences in the onset of ripening and spawning activities in females (Jones, 1980; Jones & Thompson, 1980; Barrett, 1995a).

In general, gonad size appears to be associated with the mode of reproduction. For example, *Cheilodactylus spectabilis* are benthic spawners and females have substantially larger gonads than males (McCormick, 1989). This implies that there is a degree of high precision in the spawning event and only a small quantity of sperm is required for fertilisation. In contrast, the similarity of male and female GSI values over my study indicates that *N. fucicola* are pelagic spawners for which large amounts of sperm are required to increase the probability of egg fertilisation. Similar results have been found for other pelagic species (see examples in McCormick, 1989b).

Gonads that contain gametes of all stages of development throughout the reproductive period are considered typical of fish that spawn more than once during the breeding season (McCormick, 1989b). Synchronous spawning is the most common mode of reproduction in fishes. The variety of egg size classes in combination with the presence of post-ovulatory follicles indicates that *N. fucicola* is a synchronous spawner.

3.4.3 AGE AND GROWTH

N. fucicola are a long-lived species reaching at least 25 years of age (350 mm). According to tagging studies by Barrett (1995a), the growth rate is approximately 0.5 cm per year for fish over 350 mm in length. Therefore, the largest fish examined in the present study, 400 mm, suggests that *N. fucicola* can live to at least 35 years. As other larger fish were observed, this species is likely to reach substantial ages (50 to 60 years). Aging of *Cheilodactylus spectabilis* shows this species can reach 80+ years (Choat, pers com.). Similar sized *N. fucicola* (390 mm) from Tasmania and New Zealand had substantially different ages, 17 and 25 respectively, which may reflect differences in the growth rates in different geographic regions.

In the past scale reading has been widely used as a method of aging fish but it is recognised that using scales frequently underestimates the age of older fish (Paul, 1986; Beamish & McFarlane, 1987; Carlander, 1987). For example, counts of scale annuli can sometimes underestimate the true age of fish greater than 10 - 20 years by a factor of up to 3x (Beamish & McFarlane, 1987). The consensus is that otoliths are more suitable for recording the age of long-lived species. Interpreting data from scales requires caution as many factors may affect the annuli, for example, stress of spawning, food availability, injury, pollution, fish migration, changes in salinity, available space, social factors, density, and growth responses to dramatic changes in temperature (Ross, 1987, Helfman *et al.*, 1997).

In the present study both scales and otoliths were used to age *N. fucicola*. As with other aging work on New Zealand species there were close associations between scale and otolith readings until a certain age. Paul (1976) found that with snapper, *Chrysophrys auratus*, there was a close agreement between scale and otolith readings ($r = 0.99$) until age 12, but above 12 there was virtually no agreement as there were more rings on the otolith than on the

scale. A similar problem occurred in kahawai, *Arripis trutta*, but began at age 5 (Eggleston, 1975).

As only 32 otoliths were examined in my study this may cause discrepancies and makes detailed comparisons difficult, but some general conclusions can be made. *N. fucicola* appears to have fastest growth for the first two to three years reaching approximately 100 mm in length. They appear to grow at a steady rate over their lifetime with no pronounced leveling off in older fish. Slowing down of growth after the third year may reflect the onset of a diversion of a significant amount of energy into reproduction. This growth rate is much lower than reported in Francis (1988) and is likely to be because *N. fucicola* were sampled from different geographic areas. Jones (1980) found that two geographically distinct *N. celidotus* populations had significantly different growth rates. In my study both male and female *N. fucicola* have similar growth rates, indicating that a similar amount of energy must be diverted into reproduction and growth in both sexes. Interestingly, Quignard, 1966 (cited in Dipper *et al.*, 1977) who worked on the gonochorists *Crenilabrus melops*, *Ctenolabrus rupestris* and *Centrolabrus exoletus*, found males had a significantly greater length for age than females. Growth does not appear to be asymptotic, but due to the difficulties of aging older fish this result is not conclusive.

Validation of scales showed that an annulus may be laid down in October. The pattern of annulus formation appears to be unpredictable probably due to differential growth rates. A single annulus was laid down in November of each year in *N. celidotus* (Jones, 1980). The only unequivocal method for validating the age of fish is marking with oxytetracycline (or similar markers) (Barrett, 1995a).

N. fucicola matures earlier than previously thought. Both male and female *N. fucicola* mature between 94 mm and 133 mm, or at two to three years old. This is less than 180 mm that Francis (1988) suggested. This size at maturity is similar to that of *N. celidotus* which mature between 100 - 110 mm (Jones,

1980). It appears that labrids need to reach a minimum size before investment in reproduction is worthwhile. For example, in northern New Zealand *N. celidotus* mature in their first year at 110 mm, whereas, in colder Wellington waters, *N. celidotus* do not reach maturity until they reach this size in their second or third year (Jones, 1980). It is likely *N. fucicola* mature later in the colder waters around Kaikoura as the smallest mature female was three and the smallest mature male was two years old.

CHAPTER FOUR

DIET

4.1 INTRODUCTION

The diets and foraging patterns of several New Zealand temperate rocky reef fish have been investigated, mainly around north-eastern New Zealand (see review in Jones, 1988). However, in spite of their great abundance, there have been no comprehensive studies specifically investigating the diet of *Notolabrus fucicola*. Although several authors have identified the general food items eaten by *N. fucicola* (e.g. Russell, 1973; Doak, 1978; Thompson, 1981; Francis, 1988), there have been no studies assessing seasonal variations in diet, ontogenetic change and sex differences in diet for this species.

Tropical and temperate reefs are populated with a diverse array of wrasses, most of which have powerful teeth and a pharyngeal mill adapted to crushing hard-bodied prey (Hobson, 1974; Olla *et al.*, 1974; Randall *et al.*, 1978). Labrids tend to be generalists and highly opportunistic feeders that can switch prey items when a preferred prey item is sparse, and they may exploit the activities of other fish (Randall *et al.*, 1978; Thompson, 1981). For example, octopus and goatfish (Mullidae) that feed by rooting in the substratum are often followed by labrids, which feed on dislodged prey organisms (Hobson, 1974; Randall *et al.*, 1978; McCormick, 1995). Labrids are effective predators and use different methods to capture different prey. For example, some labrids crush sea urchins by transporting them to a suitable rock and breaking them by striking with a sideways movement of the head (Keenleyside, 1979). Others use their snouts to overturn chunks of rock to expose hidden invertebrates (Randall *et al.*, 1977; Moyle & Cech, 1982). Sometimes prey is spat out and snapped out as the fish separates the food from inedible parts or broken into smaller pieces for easier swallowing (Keenleyside, 1979).

Like most labrids, *Notolabrus fucicola* is a benthic carnivore foraging over the substratum for invertebrates. *N. fucicola* has strong canine teeth and a specialised set of pharyngeal teeth, termed the pharyngeal mill, that is well

adapted for grinding and crushing the hard shells of molluscs and crabs (Marshall, 1964; Jobling, 1995; Helfman *et al.*, 1997). Several studies have mentioned a wide variety of food consumed by *N. fucicola*. These include crabs, hermit crabs, gastropods, bivalves, polychaetes, seaweeds, chitons, Munida, sea urchins, razor shells, barnacles, brittlestars and seahorses (Thomson & Anderton, 1921; Graham, 1939; Choat, 1962; Doak 1972. 1978; Thompson, 1981; Parry, 1982; Russell 1983; Ayling & Cox 1987; Francis, 1988; Paulin & Roberts, 1992).

As discussed in Chapter 2 the characteristics of the reef habitat, such as bottom topography, substrate type, and algal cover influence the abundance and distribution of reef fish (Russell, 1977). Many species undergo size-specific changes in foraging habits and diet, for example, from algal to rocky substrata (Jones, 1980, 1984b; McCormick, 1995; Gillanders, 1997). The shift in habitat often coincides with changes in morphology (Weatherly & Gill, 1987; Wootton, 1990) as their capacity to capture and ingest larger prey increases (Keenleyside, 1979). For example, in his review Jones (1988) noted changes in the diets of juveniles and adults in 11 of the 13 New Zealand species that have been examined in detail. Typically, juveniles initially feed in macroalgae that provide microhabitats for many invertebrates, such as copepods and amphipods, whereas larger fish have a stronger association with exposed rock-flat areas which support greater densities of their invertebrate prey (Leum & Choat, 1980; Kingett & Choat, 1981; Russell, 1983; Jones, 1984c, 1988; Ebeling & Laur, 1985; Shibuno *et al.*, 1997). The prey items consumed by large carnivores are generally rare within kelp forests (Choat & Schiel, 1982; Jones, 1984c; Andrew and Choat, 1985). For example, *Notolabrus celidotus* switched from feeding on invertebrates found in macroalgae when small, < 100 mm, to feeding on a range of invertebrates from algal holdfasts and on rocky substrata as adults (Jones, 1981; Jones, 1984a; Jones, 1984b). Additionally, Gillanders (1995a) found that juvenile *Achoerodus viridis*, <150 mm, foraged in shallow fringe habitats on gammarid amphipods and other crustaceans, whereas adult

fish, >200 mm, foraged in deeper turf or barren habitats on mussels and urchins.

As fish grow, their feeding rate tends to be less and the mean prey size increases (Jones, 1988). For example, the feeding rate of larger *Chrysophrys auratus*, *Cheliodactylus spectabilis*, *N. celidotus* and *A. viridis* tended to be less than that of smaller individuals (Godfriaux, 1969; Leum & Choat, 1980; Jones, 1981a, 1984a; Gillanders, 1995a). This is due to the ability of larger fish to devour larger organisms and because as fish increase in size, catching small prey such as amphipods and isopods probably requires a higher energy expenditure in relation to the amount of energy returned (Godfriaux, 1969). Moreover, larger fish with increased pharyngeal crushing strength are better able to consume larger hard-bodied prey (Jones, 1984c; Gillanders, 1995a; Helfman *et al.*, 1997).

Most generalist benthic carnivores exhibit seasonal variation in diet and feeding rate that may be due to changes in prey activity and abundance patterns (Jones, 1988). For example, Choat & Kingett (1982) observed a summer (December) peak in abundance of gammarid amphipods and an autumn (April) peak in polychaete densities, which was reflected in the diet of *Chrysophrys auratus*. Other factors that may affect the diet of reef fish include fluctuations in macroalgae abundance, water temperature, seasonal migration, and reproductive activity (Choat, 1982; Costello *et al.*, 1996). For example, the feeding intensity of the corkwing wrasse, *Crenilabrus melops* (Deady & Fives, 1995) and the ballan wrasse, *Labrus bergylta* (Dipper *et al.*, 1977) was influenced by seawater temperature with a rapid decline in winter. Dipper *et al.* (1977) found that seasonal variations in the diet of *L. bergylta* were influenced by onshore and offshore migration patterns. The mean feeding rate of *N. celidotus* followed a seasonal pattern, with the minimum occurring between July-October and the maximum rate between December-April (Jones, 1984a). Fecundity can be closely related to nutrition (Bagenal, 1978) since fecundity increases with body size. Some fish undergo a dietary change in order to

accumulate fat prior to the onset of spawning (Fishelson *et al.*, 1987) as less feeding occurs during peak reproductive times (Randall & Brock, 1959).

There is scant evidence of differences between sexes in gut fullness. Godfriaux (1969) found that female *C. auratus* and *Nemadactylus macropterus* were only slightly fuller than males. Gillanders (1995a) suggested that the slight variation in the fullness index of males and females may be because territorial males probably devote more time to defence.

The specific aims of this section were 1) to identify the main prey items of *Notolabrus fucicola*, 2) to identify temporal (seasonal) differences in their diet, 3) to determine whether fish of different sizes had different diets, 4) to determine the volume of prey taken by males and females throughout the year and 5) to investigate the relationship between fish condition and gut fullness. The composition of prey items will additionally provide information about the niche that *N. fucicola* occupies in their habitat.

4.2 MATERIAL AND METHODS

To study prey organisms, ontogenetic changes, and seasonal variation in the diet of *Notolabrus fucicola*, 30 fish per month were collected for 15 months (December 1996 to February 1998) from various areas around the Peninsula. See general methods in Chapter Three for collection procedure.

Four hundred and fifty guts were examined from fish ranging in length between 81 and 400 mm (SL). The contents of the entire digestive tract were removed, weighed and preserved in 20% alcohol. Labrids are among the 15% of teleost fish that do not possess a morphologically differentiated stomach (Gillanders, 1995a). Therefore, the entire digestive tract of *N. fucicola* was examined. The foremost part of the intestine is enlarged to form an intestinal bulb that carries

out the digestive function and has a short term storage function (Roede, 1972; Jobling, 1995).

Because there is no one method of stomach analysis that gives a complete picture of dietary importance (Hyslop, 1980), several measurements were taken to get an accurate representation of the diet of *N. fucicola*. These measurements were: (1) the frequency of occurrence of each prey item (recording the numbers of stomachs containing one or more individuals of each food category), (2) the percentage of each prey item in each gut, and (3) the weight of the gut contents. The frequency of occurrence method gives an indication of the relative number of food categories present in the population, from which preferred prey can be inferred (Hyslop, 1980). Unfortunately this method gives little indication of the relative amount of bulk of each food category present in stomachs and imparts a bias towards small numerous prey types (Berg, 1979). Recording the percentage of each prey item in each gut resolves this problem.

Each gut contained many items and therefore the entire gut contents were examined in a petri dish under a dissecting microscope. The frequency of occurrence of each item were recorded and the percentage of items in each gut were estimated. The percentage occurrence was a subjective evaluation of the percentage cover of prey items over the petri dish. Food items were identified down to species level whenever possible but the level of identification depended on the completeness of the food organism and its condition. Soft bodied prey, especially polychaetes, amphipods, and isopods, were particularly difficult to identify to species level because they were rarely in good condition. Prey items in an advanced state of digestion were not included in analysis as it was not possible to determine prey type. Detritus present in the gut included sand, stones, seaweed and coralline algae, were recorded but were no doubt ingested accidentally with the prey.

To determine if gut fullness differed over the study and between the sexes, the fullness index (FI) was calculated from the formula $FI = W1/W2 \times 100$, where W1

= weight of ingested food and W_2 = total fish weight (Berg, 1979). The condition factor (K) is a coefficient used to measure variations in fish weight associated with fish length. The condition factor for all fish over the study was calculated from the equation $K = W(100)/L^3$, where W = weight (g), and L = length (cm). If the K values are high then plenty of food is available (Moyle & Cech, 1982).

Analysis of variance was used to test whether the major prey categories were ingested in significantly different proportions by fish over the study period.

4.3 RESULTS

4.3.1 PREY ITEMS

Notolabrus fucicola were found to be generalist predators with a wide variety of prey in their diets. There were forty-eight species of prey items identified from twelve families. But also many other unidentifiable items (See Appendix One for a description of all dietary items). The main prey items were bivalves, decapods, amphipods, and gastropods but found in smaller amounts were salps, isopods, polychaetes, limpets, chitons, sea urchins, and fish (Figure 4.1). Bivalves made up the largest volume in the guts (25%) followed by crabs (8%) and amphipods (6%) (Figure 4.2). The importance of carrying out two methods of analysis can be seen from the different results given in Figure 4.1 and 4.2.

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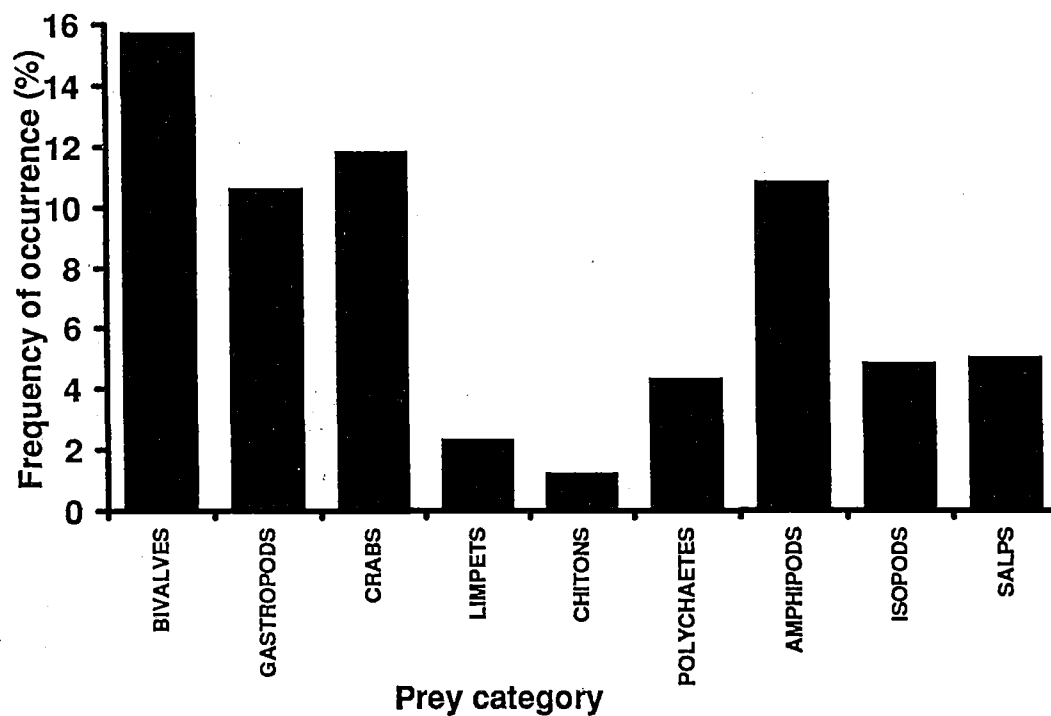


Figure 4.1 Frequency of occurrence of prey items in the gut of all *Notolabrus fucicola* pooled across the study period (Dec 1996 to Feb 1998).

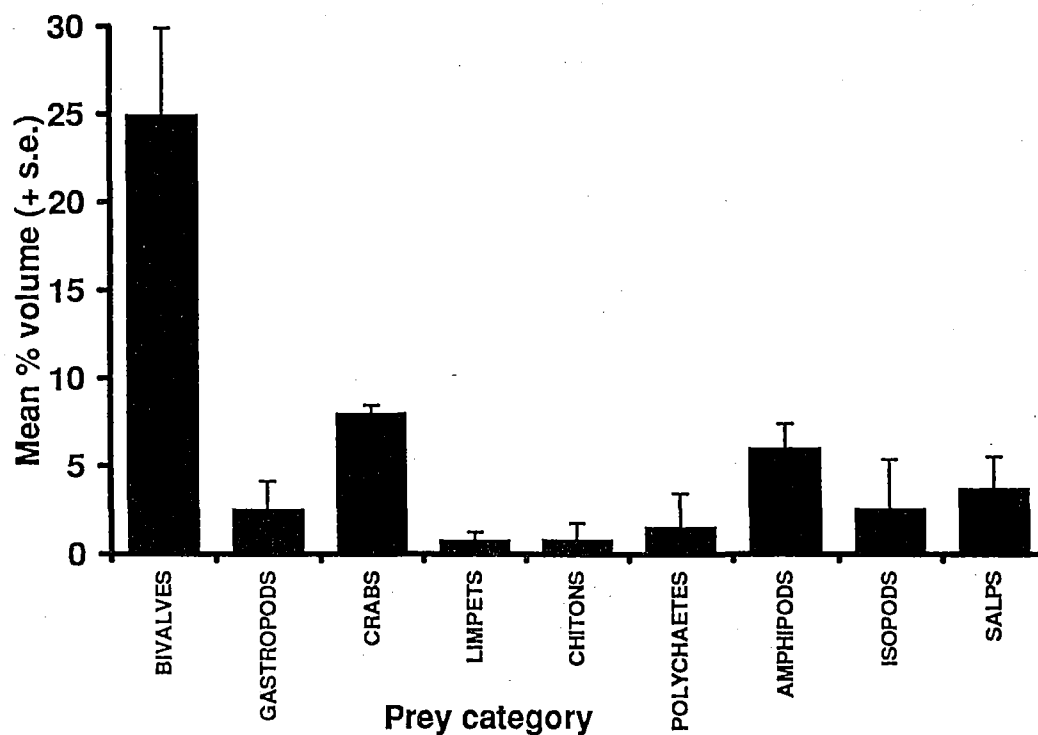


Figure 4.2 Mean percentage volume (+ s.e.) of nine major prey items found in the gut of all *Notolabrus fucicola* sampled from Dec 1996 to Feb 1998.

The ribbed mussel, *Aulacomya maorianus*, was the main bivalve occurring in 13% of all fish with the hairy mussel *Modiolus aerolatus* (1.7%), and the blue mussel *Mytilus edulis aoteana* (1%), present in small amounts. The red rock crab, *Plagusia chabrus*, was the dominant decapod accounting for 2.2% of total food volume, which is comparable to what Russell (1971) found. Other crabs that made up a combined total of 3% of gut volume were *Notomithrax peronii*, *N. ursus*, *N. minor*, *Notomithrax* sp., *Trichoplatus huttoni*, *Eurynolamprus australis*, *Leptomithrax* sp., *Pilumnus novaezelandiae*, *Hemigrapsus edwardsi*, *Ovalipes catharus* and *Halicarcinus varius*. Unidentified crab remains (mainly legs) accounted for 7% of gut volume. The high proportion of unidentified crab legs is likely to be due to the observed labrid behaviour of ripping legs off the carapace (Graham, 1956). Choat (1962) observed that crustacean appendages were fairly common in the gut. Other Crustacea found in guts included *Jasus edwardsii* (0.2%), *Euphausid* sp. (0.3%), Chthamiliid barnacles (0.3%), crab larvae (0.2%) and isopods (5%) represented by the families Valvifera, Asellota, Anthuridae, Flabellifera and Oniscoidea. Amphipods, mainly Gammaridae, accounted for 11% of total gut volume.

Gastropods occurred in 11% of fish but made up only 2.2 +/- 1.7% of the total percentage volume (Figure 4.1 and 4.2). Species identified in guts were *Zeacumantus subcaratus*, *Z. ?carinatus*, *Z. lutulentus*, *Trochus viridis*, *Antisolarium egeum*, *Maurea pellucida*, *Cominella glandformis*, *Buccinulum lineum*, *Soletellina nitida* and *Notoacmea pileopsis*. Limpets and chitons occurred in only 2.7% of guts and made up 2% of gut volume. The main species were the ornate limpet, *Cellana ornata*, the radiate limpet, *Cellana radians* and the serpent chiton, *Sypharochiton pelliserpentis*. Unfortunately, the majority of gastropod shells were fragmented which made identification impossible. Unidentified gastropod shells were found in 9.9% of fish guts.

Polychaetes were found in 4% of the fish sampled and comprised only 2% of the gut volume. Many polychaetes were in an advanced state of digestion and therefore could not be identified below ordinal level.

Salps were present in 4.3% of the guts and consisted of 3.8 +/- 1.8% of the volume. Minor items included the sea urchin *Evechinus chloroticus* (1%), turbellaria, *Chromoplana* sp. (0.1%), unidentified fish species (0.2%), a seahorse (0.1%), unidentified bones (0.8%), ascideans (0.7%) and a squid, *Nototodarus* sp. (0.1%). Stones (4.7%) and seaweed (7%) were found, usually in very small quantities, and are likely to have been incidentally ingested while fish fed on other prey. Empty guts were relatively rare and were only found in 0.7% of fish.

4.3.2 ONTOGENETIC CHANGES

There were changes in the diet with increasing fish size (Figure 4.3, 4.4). Both the frequency of occurrence and mean percentage volume demonstrated that the principal prey of *N. fucicola* <180 mm were soft-bodied organisms, mainly amphipods and isopods. Although polychaetes occurred in most of these smaller fish the average volume was relatively small (Figure 4.4). From 180-270 mm there was a transition in the diet away from soft-bodied prey towards hard-bodied animals such as crabs, gastropods and bivalves. The exception were salps that occurred in about 20% of fish but had a mean volume of approximately 40%. Fish > 270mm preyed almost exclusively on hard-bodied animals. The amounts of amphipods, isopods and polychaetes decreased in percentage occurrence with increasing fish size while bivalves, crabs, gastropods showed an increase.

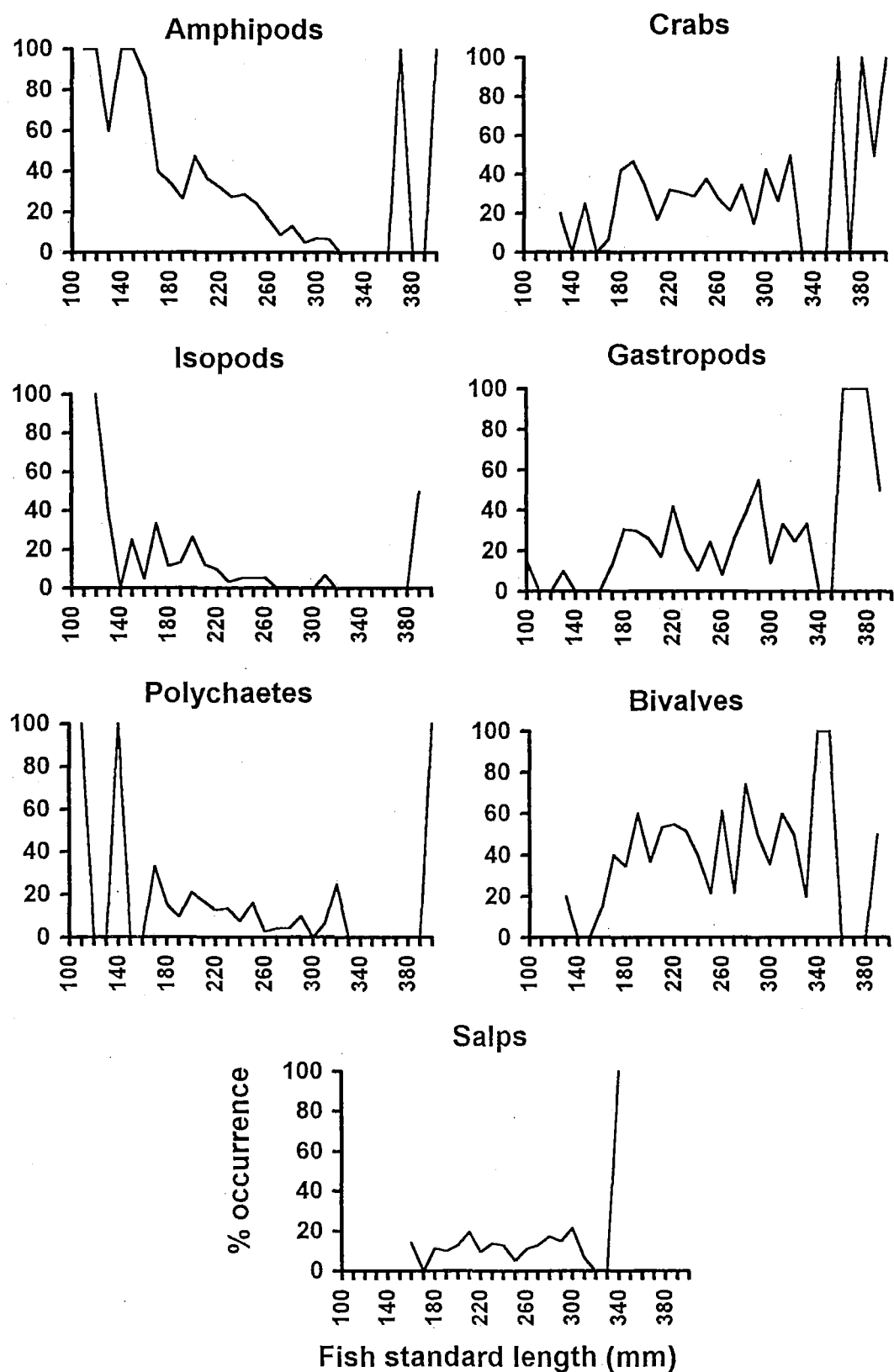


Figure 4.3 Percentage of occurrence of seven major prey categories pooled across all seasons in all *Notolabrus fucicola* divided into 10 mm size classes.

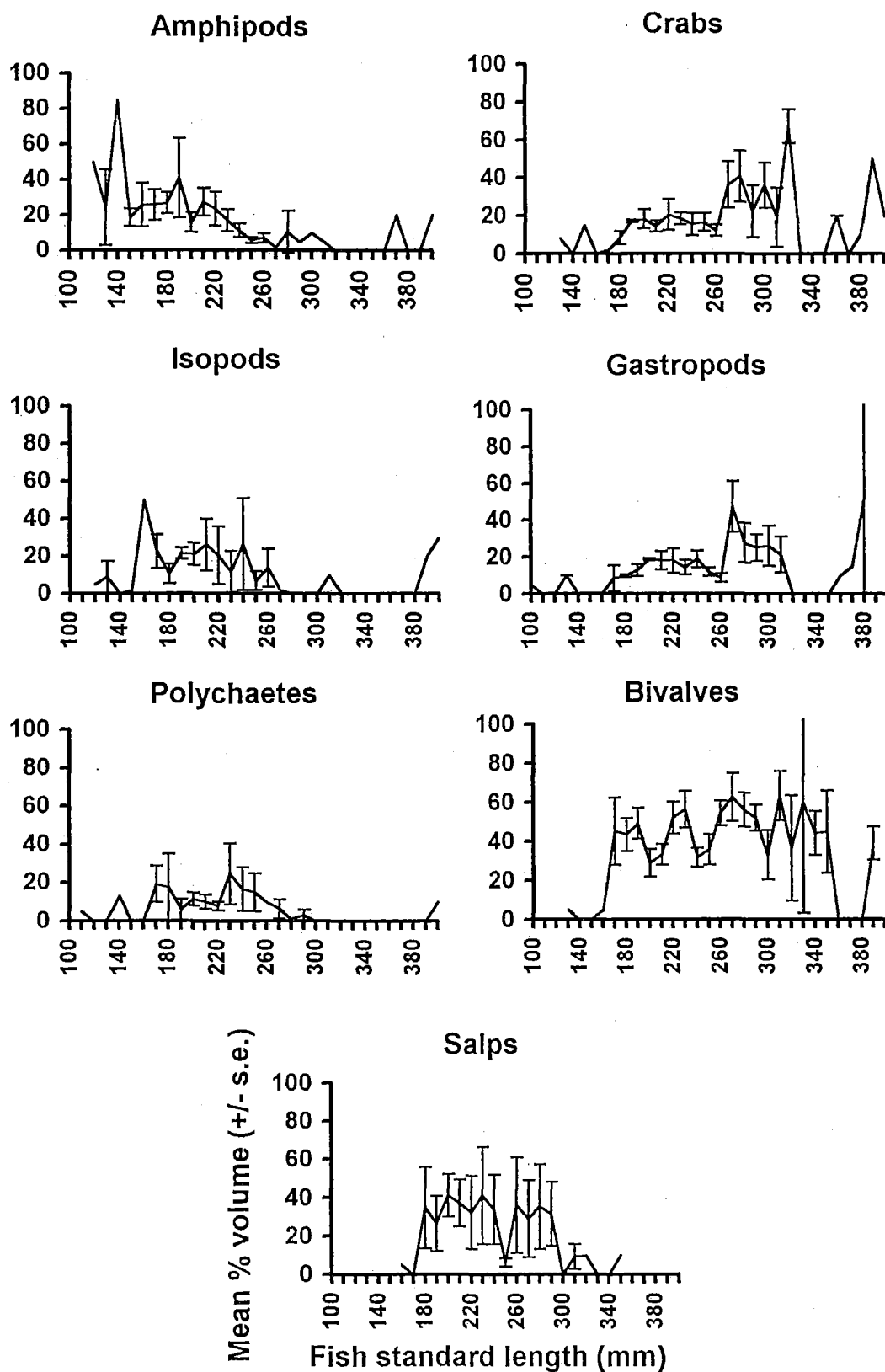


Figure 4.4 Mean percentage volume (\pm s.e.) of seven major prey categories pooled across all seasons in all *Notolabrus fucicola* divided into 10 mm size classes.

4.3.3 SEASONAL PATTERNS

Almost all prey categories varied significantly in their percentage volume over fifteen months (Table 4.1). Only polychaetes ($F = 1.45$, $p = 0.321$) and gastropods ($F = 1.75$, $p = 0.298$) showed no significant variation over time (Table 4.1 B and E). Chitons ($F = 1.96$, $p = 0.02$) and isopods ($F = 1.98$, $p = 0.018$) were not significant at $p < 0.01$ (Table 4.1 D and G). Peak densities of amphipods occurred in summer (Dec 1996, Jan 1997 and Feb 1998) and declined rapidly after the January 1997 peak (Figure 4.5b). Salps were only present in any numbers over the summer months, mainly Nov-Dec and March 1997 (Figure 4.5b). Bivalves were the dominant prey from Feb-Aug 1997 (Figure 4.5a). The peaks in prey are likely to be due to seasonal variation in prey availability.

Table 4.1 A - I: Analysis of variance showing differences in prey items in the gut of *Notolabrus fucicola* over time.

A: BIVALVES

Source of variation	df	MS	SS	F-ratio	p-value
Time	14	14718	14732	16.50	0.000
Residual	435	891.85	387956		
Total	449				

B: GASTROPODS

Source of variation	df	MS	SS	F-ratio	p-value
Time	14	160.18	174.18	1.17	0.298
Residual	435	137.32	59735		
Total	449				

C: LIMPETS

Source of variation	df	MS	SS	F-ratio	p-value
Time	14	45.55	59.55	2.16	0.009
Residual	435	21.13	9189.47		
Total	449				

D: CHITONS

Source of variation	df	MS	SS	F-ratio	p-value
Time	14	35.78	49.78	1.96	0.020
Residual	435	18.29	7956.23		
Total	449				

E: POLYCHAETES

Source of variation	df	MS	SS	F-ratio	p-value
Time	14	52.16	66.16	1.14	0.321
Residual	435	45.77	19911		
Total	449				

F: AMPHIPODS

Source of variation	df	MS	SS	F-ratio	p-value
Time	14	1869.6	1883.62	8.40	0.000
Residual	435	222.52	96797		
Total	449				

G: ISOPODS

Source of variation	df	MS	SS	F-ratio	p-value
Time	14	195.28	209.28	1.98	0.018
Residual	435	98.53	42862		
Total	449				

H: CRABS

Source of variation	df	MS	SS	F-ratio	p-value
Time	14	1489.9	1503.87	4.85	0.000
Residual	435	307.39	133716		
Total	449				

I: SALPS

Source of variation	df	MS	SS	F-ratio	p-value
Time	14	674.99	688.99	3.67	0.000
Residual	435	184.17	80114.2		
Total	449				

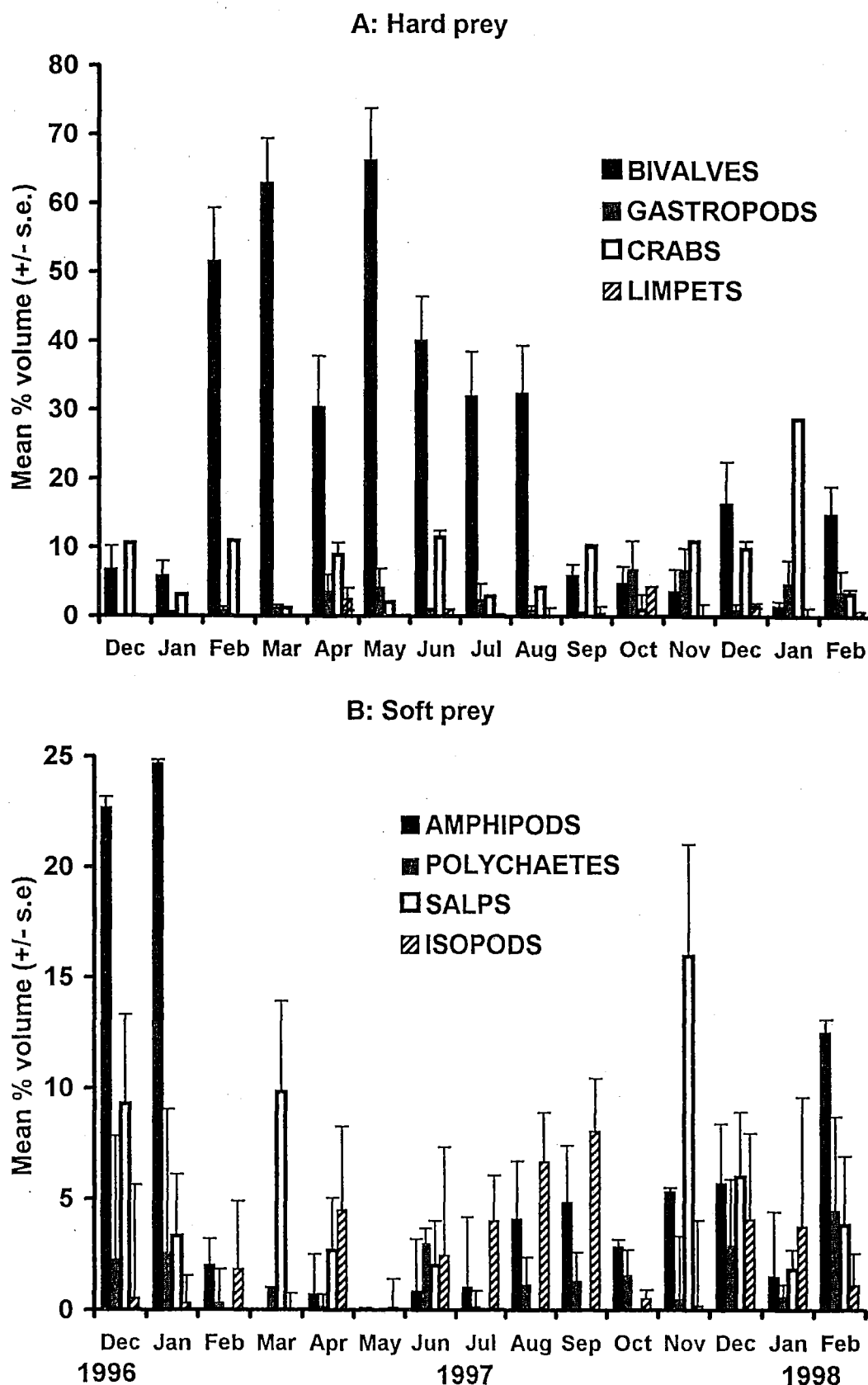


Figure 4.5 Mean percentage volume (+ s.e.) of A: Hard prey and B: Soft prey in the guts of *Notolabrus fucicola* sampled around Kaikoura from Dec 1996 to Feb 1998. Note the different y-axes.

4.3.4 GUT FULLNESS AND CONDITION FACTOR

The gut fullness of *N. fucicola* changed on a seasonal basis with a gradual decline from summer to winter followed by an increase for both sexes over spring (Figure 4.6). The overall patterns were similar for both sexes except in January 1997 where females had a substantially higher fullness index. There was a significant difference over time in the condition factor for both males ($F_{14,266} = 4.73$, $p < 0.001$) and females ($F_{14,157} = 6.59$, $p < 0.001$). The values varied similarly for both sexes.

Condition factor values were highest in January and February 1997 following the conclusion of the spawning season. The lowest values were recorded in August for females and September for males coinciding with the peak spawning period (Figure 4.7). The second summer period (Dec - Feb) did not have the high values of the previous summer.

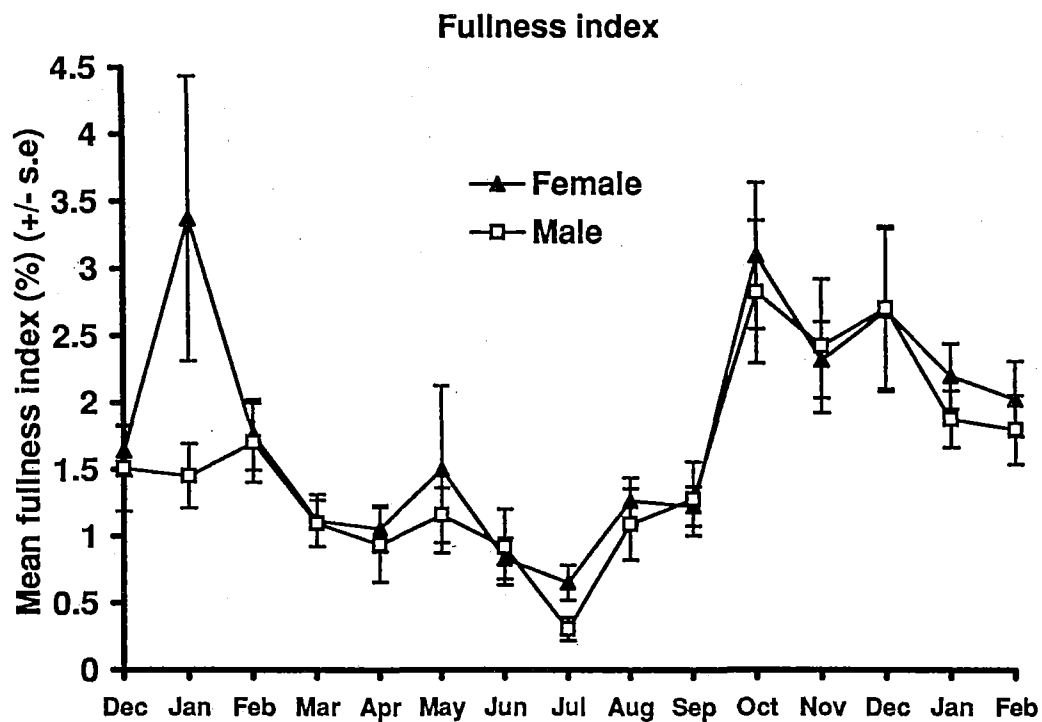


Figure 4.6 Mean fullness index of male and female *Notolabrus fucicola* sampled around Kaikoura from Dec 1996 to Feb 1998 (+/- s.e.).

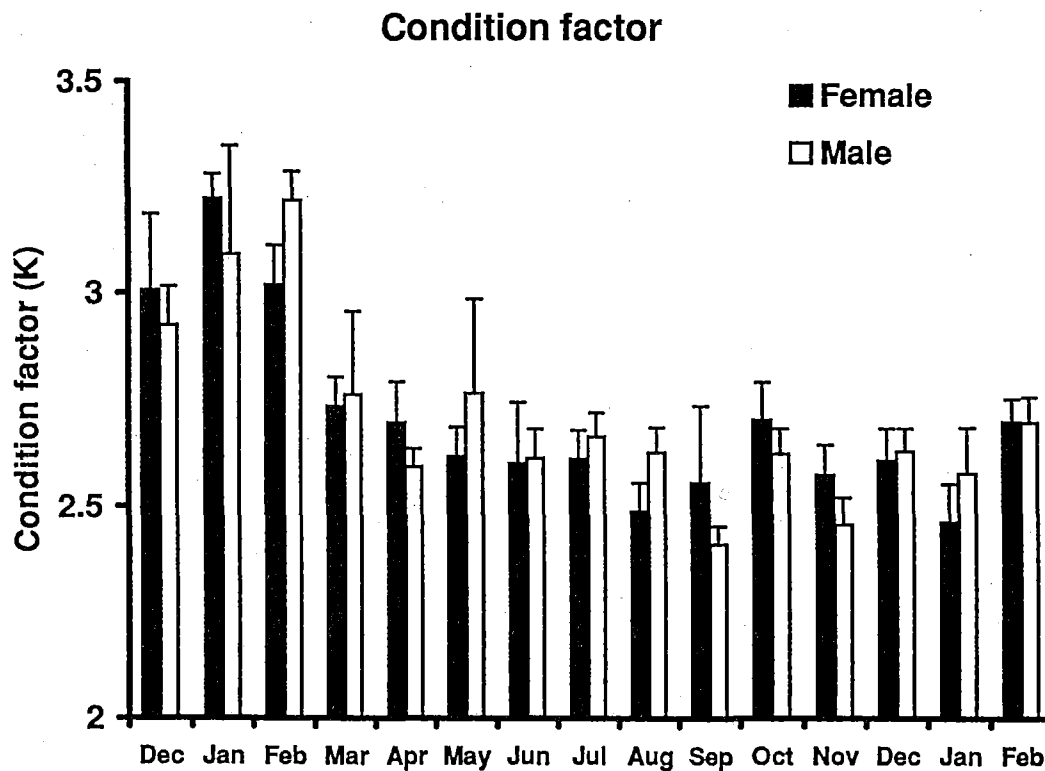


Figure 4.7 Condition factor (K) (+ s.e.) for male and female *Notolabrus fucicola* sampled around Kaikoura from Dec 1996 to Feb 1998.

4.4 DISCUSSION

Notolabrus fucicola is primarily a carnivorous feeder, taking a varied diet with bivalves and crustaceans predominating. The results of this study vary from previous reports on the diet of *N. fucicola* (Russell, 1971; Thompson, 1981). Russell (1971) and Thompson (1981) report that crabs and hermit crabs were the main prey items with bivalves only minor items (2%). Although crabs ranked second in the overall diet, bivalves were the predominant prey items identified in this study. The differences in diet may reflect seasonal variations in prey composition, differences between geographic regions, and the size classes collected (Godfriaux, 1969; Jones, 1984a; McCormick, 1995). For example, Russell (1971) only sampled 15 fish, all > 170 mm, which may account for the absence of amphipods in his study. The areas sampled may influence results. For example, Cowen (1986) reported that *Semicossyphus pulcher* fed on macroinvertebrates (especially urchins) on barren grounds and on smaller crustacean elsewhere. A seasonal variation in prey items was recorded over this study, suggesting that the time of sampling influences the prey categories present. Other common rocky reef invertebrates were not utilised as much as expected, for example, sponges, ascidians, hydroids and anemones (Russell, 1983). Russell (1983) stated that these invertebrates are likely to be of low nutritional value or unpalatable.

N. fucicola has a generalised feeding habit and shows flexibility in its diet, feeding on whatever is abundant. As for most benthic carnivores, temporal changes in diet were found for *N. fucicola*, with almost all prey items showing significant variation over time. Some species displayed peaks in the gut [?] over the study. For example, summer peaks occurred in amphipods and salps, and there were high volumes of bivalves from February to August. Kingett and Choat (1982) observed a similar pattern of abundance for amphipods. Variations may be caused by seasonal changes in prey populations relating to activity and abundance patterns (Jones, 1988) or fluctuations in macroalgal abundance and water temperature (Choat, 1982).

A shift in prey choice is a common occurrence in reef fish (Jones, 1988) and is evident for *N. fucicola*. Smaller fish, <180 mm, feed mainly on soft-bodied animals, predominantly amphipods and isopods, while fish >180 mm feed mostly on crabs, bivalves and gastropods. One interpretation of this dietary shift is a change in foraging habitat from macroalgae to rocky areas. However, as discussed in Chapter Two, *N. fucicola* does not show significant variation with size across depth zones. It seems that fish would be able to forage efficiently over both algal and bare rock habitats, as these habitats occur at most depths. Therefore, they are unlikely to need to partition habitats for feeding. Another reason for a lack of depth related change may be because bivalves, the main prey items of larger fish, are filter feeders and are more likely to occur in shallower waters where there is more phytoplankton available. Even though there is no evidence of size change associated with depth, behavioural observations indicate that the largest fish (>400 mm) spend more time swimming and foraging over rocky areas. Large fish (>300 mm) were observed swimming over intertidal rock flats, a behaviour seen in Australia where *N. fucicola* feeds on intertidal limpets (Parry, 1982; Odeja & Dearborn, 1991). Results from diet analysis showed that this species fed on some strictly intertidal species, such as *Cellana* sp. and *Zeacumantus subcaratus*.

The gut fullness index displayed seasonal variation with a gradual decline from summer to winter followed by an increase during spring. A similar pattern was observed for both males and females, except in January 1997 where female means were substantially higher. There was little evidence of sex differences in gut fullness, similar to the findings of Godfriaux (1969). Differences in fullness and fish condition reflect changes in the feeding rate throughout the year. These changes generally relate to seasonal variation in prey, low water temperature or reproductive activity (Choat, 1982). The explanation for the change in the fullness index in *N. fucicola* throughout year is likely to be related to colder water temperatures. For example, Jones (1980) found that the feeding rate of *N. celidotus* was lowest in the winter months between July and October

and highest in summer. Alternatively, the rate of feeding activity can decrease or cease as the fish become reproductively active (Randall & Brook, 1960; Deady & Fives, 1995). *N. fucicola* may have been accumulating fat over the summer prior to the onset of spawning as there was a noticeable decline in the fullness and condition from the initial highs over summer until the onset of spawning.

The condition factor has been shown to vary seasonally in several different fish species (Jones, 1970). The present study found significant variation over time with K showing a pattern resembling the fullness index with a peak in summer then declining towards winter. This decline may have been related to the onset of spawning as Habib (1971) found the condition factor for *Uranstoma richiei* showed an inverse relationship with the gonad cycle. The K values did not increase over the second summer period (Dec - Feb). This could be caused by the El Nino weather pattern that may have reduced the amount of available invertebrates for *N. fucicola*. Additionally, the condition factor may be affected by bias in sampling selection, environmental conditions, food supply, and time of collection. Fish were collected at various times of the day in this study, so to reduce bias and provide more conclusive information regarding the condition factor and gut fullness, it would be more appropriate to sample fish at a similar time.

There is considerable debate about the degree to which fish populations affect the abundance of invertebrate fauna on temperate reefs (Choat, 1982; Jones, 1988). Fish may play an important role in influencing the distribution, species composition and abundance of invertebrate reef species as they have the ability to forage over a wide range and consume large numbers of invertebrates (Choat & Kingett, 1982; Russell, 1983; McCormick, 1995; Helfman *et al.*, 1997). For example, in areas where *Parika scaber* were experimentally excluded, there was a substantial increase in the cover of sponges, ascideans, and polyzoans (Ayling, 1981). Cowen (1986) suggested that *Semicossyphus pulcher* at medium and high densities could regulate or overexploit sea urchin

populations. However, Choat & Kingett (1982) and Choat & Ayling (1987) concluded that reef fish are unlikely candidates for maintaining the structure of algal turf invertebrate communities and kelp forests by preying on invertebrates. They found little evidence of a fish predation effects on either the densities of invertebrates or the timing of abundance peaks in northern New Zealand. Choat & Kingett (1982) suggested that seasonal changes in the abundance of invertebrates occurs independently of fish predation. Temperate marine fish may have a negligible effect on the benthic community due to the complexity of natural substances providing refuges for prey (Hixon, 1986). Choat (1982) stated that "the potential for temperate fishes to have general and unequivocally recognised effects on the distribution and abundance of their benthic prey is not apparently realised. If temperate fishes do have a significant influence on benthic organisms then this fact has not found its way into the general ecological literature." Even relatively recently, Gerking (1994) wrote that "it is difficult to appraise the effect of bottom feeding fish on the benthic community structure at this time." Experimental tests to determine the effect of *N. fucicola* on the benthic community are not feasible because of their wide diet and extensive ranging behaviour.

CHAPTER FIVE

BEHAVIOUR

5.1 INTRODUCTION

To gain an understanding of the life history and social structure of a species it is necessary to understand how it spends its time. This is quite easy if you are studying in areas with warm water temperatures, calmer conditions and greater visibility. However, when it comes to studying a large fish in the cold, often murky waters around Kaikoura the task of formulating a time budget becomes a little more difficult. This chapter is intended to identify the main activities of *Notolabrus fucicola*, as the literature provides sketchy information on the general behaviour patterns of this species. Barrett (1995a, b) has carried out behavioural work on *N. fucicola*, investigating movement patterns of this species. Although I am looking at all behavioural activities of *N. fucicola*, I am mainly investigating the territorial behaviour of this species, the rationale behind territoriality, and nocturnal behaviour.

Little¹⁵ known about the behaviour of marine fishes in habitats other than coral reefs as there have been few behavioural studies on temperate marine species (Grant, 1997). Most behavioural studies have focused on territorial behaviour and the reasoning behind it. The most common definition in the literature to define territorial behaviour is 'any defended area' (Mater & Lott, 1995). Territories are located within home ranges that are larger undefended areas that a fish uses in its daily activities (Helfman *et al.*, 1997). All reasoning for territorial behaviour involves competition for some limiting resource, such as food, shelter, mates, nest sites, spawning sites and offspring (Stevens & Zerba, 1981; Warner, 1984; Ross, 1990; Helfman *et al.*, 1997). A fish will only defend a territory if the fitness benefits of defence exceed the costs. Benefits of having a territory include higher foraging efficiency, increased mating and spawning success, survivorship and offspring survival, and lower rates of predation than non-territorial fish. Costs include time and energy spent on antagonistic activity and the increased risk of injury (Grant, 1997). For example, when faced with greater numbers of IP males, territorial *Thalassoma bifasciatum* males

increased time spent in defence, decreased time spent in courtship and suffered a lower mating efficiency while courting (Warner & Hoffman, 1980b).

Territorial behaviour is relatively common in teleosts, occurring in 67% of the families of fishes whose behaviour was well described. Defence of spawning sites, mates or offspring occurred in 78% of the families of fishes and did not differ among coral, freshwater and marine fauna (Grant, 1997). However, the incidence of feeding territories differed between tropical and temperate species. Only 6% of the marine families of eastern Canada defended a food source compared to 68% of coral-reef families (Grant, 1997). This low percentage of food defence may be because food resources of most temperate fish can be widely distributed so they forage over a wide home range instead of defending a territory (Warner, 1984). Grant (1997) suggested that spawning sites, mates or offspring were more economically defensible than food.

Males often only become territorial during the breeding season when they defend display sites from other males (Warner, 1984; Gerking, 1994). For example, large male *Halichoeres garnoti* are territorial particularly when spawning, but they are weakly territorial towards each other outside spawning periods (Warner & Robertson, 1978; Robertson, 1981). This behavioural change is because territoriality males have more reproductive success than non-territorial males. Non-territorial males usually form temporary breeding territories where females gather and generally spawn with one of the competing males (Dipper & Pullin, 1979; Gross, 1984).

Home ranges are often very large in temperate reef fish. For example, the home range of *N. celidotus* may be up to 800m² (Jones, 1981a, b), 2500 to 5000m² for the clown fish, *Halichoeres garnoti* (Thresher, 1979) and 100 x 25 m for *Notolabrus tetricus*, *Pictilabrus laticlavius* and *Pseudolabrus psittaculus* (Barrett, 1995b). The home range of *N. fucicola* is large and is reported to be between 300 and 600 m² (Thompson, 1981) and at least 100 X 25 m (Barrett,

1995b). *N. fucicola* range over the whole reef on a daily basis, with their ranges overlapping those of numerous others (Barrett, 1995b).

Generally interspecific interactions among reef fish are rare and usually occur for food resources (Thresher, 1979; Stephens & Zerba, 1981). For example, Godfriaux (1970) compared six New Zealand temperate reef fish and found that active interspecific competition between predators for a prey species was rare, and if present, not severe. Conversely, Thompson & Jones (1983) suggested that certain size classes of *N. celidotus* compete with the blennoid, *Forsterygion varium* for food. Interspecific aggression is unusual but does occur between *N. fucicola* and other species (Ayling, 1980). Graham (1956) noted that *N. fucicola* were the most domineering of all the fish he kept in captivity; 'other larger fish were not able to hold their own against these quarrelling, biting, fighting fish.'

Wrasses are predominantly active during the day and they are usually the first diurnal fishes to retire to shelter for the night and among the last to appear in the morning (Hobson, 1965, 1974; Roede, 1972; Ebeling & Bray, 1976; Leum & Choat, 1980; Stephens & Zerba, 1981; Nelson, 1984; Helfman, 1986; Howard, 1989). Wrasses are credited with possessing the faculty of sleeping which is apparently rare amongst fishes (Helfman *et al.*, 1997). At night wrasses can lie quietly on their sides (Roughly, 1961; Roede, 1972; Nelson, 1984) in crevices among rocks (Graham, 1956; Randall *et al.*, 1978), or buried in sand (Doak, 1972; Roede, 1972; Howard, 1989). Wrasses, including *N. celidotus* and *N. fucicola*, are reported to secrete a thick, transparent mucous envelope around themselves at night (Byrne, 1970; Russell, 1971). There has been much speculation about the benefits of this envelope but little investigation (Helfman *et al.*, 1997). Two theories include defence against predation (Winn & Bardach, 1959) or an incidental by-product of mucous production that occurs during the day but does not accumulate because the fish are continually active (Helfman *et al.*, 1997). Choat (1962) attempted to capture *N. fucicola* at night but was unsuccessful.

5.2 METHODS

The activities of randomly selected fish were recorded for five months at several sites around the Kaikoura Peninsula, for a total of 30 hours observation. Fish were followed by snorkeling and behavioural activities were recorded on a perspex slate while hovering 1-3 metres above them. It was difficult to follow fish using SCUBA as air bubbles often spooked fish. Each fish was followed for as long as possible, approximately 3 - 4 minutes, with activities recorded at 10 seconds intervals. At the beginning of each observation period the standard length was recorded and the colour phase identified. Dives were conducted when the water visibility was greater than three metres.

Behaviour categories were divided into two sections, maintenance and interactions. Maintenance categories were separated into 1) swimming, actively moving > 5 cm above seaweed or rock, 2) swimming in weed (< 5 cm from seaweed), 3) swimming over rock (< 5 cm), 4) resting in seaweed, 5) resting on rock, 6) hovering, and 7) feeding, actively consuming prey.

Interactions were divided into 1) aggressive displays, where one fish acts aggressively towards an opponent, and 2) submission, where the subject is chased by another fish (For a summary of behaviour categories, see Table 3.3).

To investigate territorial behaviour, a sea urchin (*Evechinus chloroticus*), was opened in 1) areas where there was a territorial fish present and 2) in areas where there was no territorial individual. Both situations were carried out three times at three different sites.

To investigate nocturnal behaviour two night dives using SCUBA were conducted.

5.3 RESULTS

The average percentage of time spent on each behavioural activity were as follows: swimming, 37 +/- 7.3, swimming in seaweed, 35.8 +/- 5.1, swimming over rock, 5.1 +/- 3.8, resting in seaweed, 5.2 +/- 2.6, resting on rock, 1.7 +/- 1.0, feeding, 1.4 +/- 1.0, hovering, 3.4 +/- 1.7, aggressive displays, 2.7 +/- 1.0 and submissive displays, 0.1% (Table 5.1).

When separated into four size classes (90 mm) there was little difference in activities with all fish spending the majority of their time swimming 1 - 2 m above the substrate (34.7 - 40%) or swimming in weed (27.8 - 42.1%). The main differences involved the large (> 400 mm) fish which spent more time swimming over rock and less time hovering than other size classes. Interestingly these large fish displayed no aggressive behaviour. The feeding rate between different size classes varied from 0.6 - 2.4% of the time budget (Figure 5.1).

Table 5.1 Behaviour categories, codes and the mean percentage of time (+/- s.e.) spent on each activity for all *Notolabrus fucicola* observed from September 1997 to February 1998 (n = 464).

Behaviour categories	Code	Mean % time (+/- s.e)
Swimming	S	37.0 +/- 7.3
Swimming <5 cm from seaweed	SW	35.8 +/- 5.1
Swimming <5 cm from rock	SR	5.1 +/- 3.8
Resting in seaweed	RW	5.2 +/- 2.6
Resting on rock	RR	1.7 +/- 1.0
Feeding	F	1.4 +/- 1.0
Hovering	H	3.4 +/- 1.7
Aggressive displays	A	2.7 +/- 1.0
Submissive displays	SB	0.1

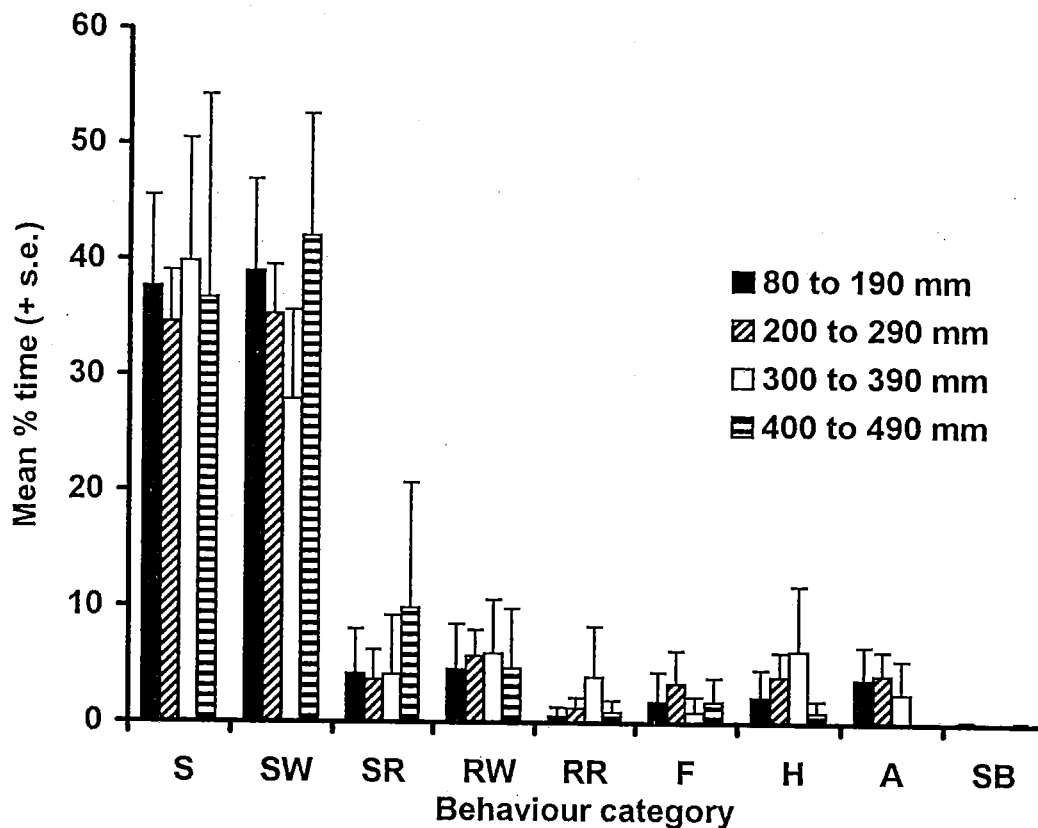


Figure 3.9 Mean percentage of time (+ s.e.) spent on nine behaviour categories for *Notolabrus fucicola* in four standard length classes observed from September 1997 to February 1998 (Table 3.3 for behaviour category codes).

Many *N. fucicola* displayed aggressive behaviour that appeared to be related to territorial ownership. Of the 464 fish followed 96 (20%) displayed some form of aggressive behaviour. There was no obvious association between colour phase and size with aggressive behaviour, as fish of all sizes and colour phases exhibiting territorial behaviour. For example, 150 mm IP fish, were observed to chase much larger 300 mm TP fish. The intruder always fled regardless of size and no resident was seen to be displaced in a territorial dispute. All aggression was accompanied by the same behavioural action where the dorsal fin was raised and the aggressor rapidly swam towards the intruder. Confrontations were usually brief (< 5 seconds) and rarely involved a fight. Border disputes between adjacent territorial fish were observed (eleven times). Both fish engage in aggressive displays and a series of short chases

around the borders of the territory. Neither fish appeared submissive and both retired to the seaweed after the confrontation.

Interspecific aggression, although rare, was occasionally observed (ten observations) towards *Notolabrus celidotus*, *Odax pullus*, *Aplodactylus arctidens* and *Arripis trutta*. The typical aggressive display occurred but was not as vigorous or prolonged as conspecific aggression.

It was not possible to visually determine the sex of territorial fish and therefore it was difficult to make conclusions about the spawning function of territories. Of five fish that were identified as territorial before spearing four were females and one a male. The territory size appeared to be relatively small, approximately 4 x 4m.

Investigating territorial behaviour using the sea urchin, *Evechinus chloroticus*, revealed interesting results. In areas with a territorial fish, intruders were constantly chased away from the urchin and out of its territory. As can be imagined this task became increasingly difficult with increasing numbers. When an urchin was opened in areas without a territorial fish many *N. fucicola* arrived to feed with little aggression between feeding fish.

Areas where *N. fucicola* were found during the day were ^{free} absent of them at night. Although four divers spent an hour on two separate occasions looking in cracks and seaweed for *N. fucicola*, only one was ever seen at night lying in a crack.

5.4 DISCUSSION

Most fish spent over a third of their time associated with seaweed, either swimming or resting. The close association *N. fucicola* has with seaweed, for shelter, food and recruitment, was discussed in Chapter Two. As expected larger fish (400 - 490 mm) spent twice as much time as smaller fish swimming over rock substrata as this is where their preferred prey is found. However, it is surprising that fish in 300 - 390 mm size range were not observed to swim over rock more often, as they feed on similar items.

Behavioural observations indicated that the feeding rate between different size classes varied from 0.6 - 2.4% of the time budget. Although this is small percentage of the time budget, it is likely that *N. fucicola* spends a similar amount of time foraging as *N. celidotus*, 80 - 90% (Jones, 1984a). Although it was difficult to observe fish feeding in weed it is evident from stomach content analysis that they consume items in seaweed because small fragments of weed were found. *N. fucicola* are opportunistic and were observed feeding on prey items exposed by octopus. Numerous times after feeding *N. fucicola* were seen to spit prey out and pick out parts floating in the water column.

Aggressive displays, characterised by fin raising, occurred often but only represented a small percentage of the total time budget, $2.7 \pm 1.0\%$. This is higher than $1.6 \pm 0.2\%$ observed between TP *N. celidotus* males (Jones, 1981a, b). Fin erection plays a dominant role in visual displays, probably because the movement associated with their erection is particularly eye-catching and increases the apparent size of the fish.

While the function of territorial behaviour in *N. fucicola* is unclear, aggressive displays are likely to be for defence of either food, shelter, spawning sites or offspring. It would be expected that territorial behaviour of *N. fucicola* would be for spawning sites as this appears to be the most common reason for territoriality. For example, defence of spawning sites or mates occurred in 78% of families in

which behaviour was described. However, several observations suggest that territories are not for spawning. Fish were observed to display territorial behaviour well after spawning had ceased in late February. Fish in small size classes were observed to display aggressive behaviour. If territoriality was for defense of spawning sites then it would be expected that very large fish would be the dominant territorial fish on the reef. However, large fish, > 400 mm, displayed no aggressive behaviour. In addition, this species is monochromatic suggesting male *N. fucicola* do not attract females. Moreover, the majority of territorial fish speared were female. As no spawning was observed in the present study it is unwarranted to conclude that territories are used for spawning.

It would be unexpected that *N. fucicola* defends a food resource as Grant (1997) found only 6% of marine fish in eastern Canada defended a food source. This may be because the food resources of temperate fish are widely distributed so they forage over a wide home range instead of defending a territory (Warner, 1975b). They are generalist predators with a wide range of dietary items so are likely to forage over a wide range. However, several observations suggest aggression may have been in defence of particular food resources. Fish of all sizes defended feeding areas against all intruders that is consistent with Robertson (1981) who found *Halichoeres garnoti* of all sizes defended their feeding areas against equal sized conspecifics. *N. fucicola* displayed aggression towards *Notolabrus celidotus*, *Odax pullus*, *Arripis trutta* and *Aplodactylus arctidens*. While almost all interspecific interactions between *N. celidotus* and other species appeared to relate in some way to food (Jones, 1984a), this is unlikely to apply to *N. fucicola* as they were aggressive towards a non-competitive herbivorous species. Moreover, defended areas seemed to be approximately 4 x 4 m which is very small. On average, feeding territories were 11 times larger than territories used for reproduction for most reef fish (Grant, 1997). This small territory size may be because food resources may be sufficiently abundant in these small defended areas. Furthermore, territorial fish

defended areas where sea urchins were opened, suggesting defence of a food source.

Territorial behaviour may only occur if the population is stable. Barrett (1995a) observed, in Tasmanian populations, that while males were frequently involved in chases during the breeding season, there was little evidence for territorial behaviour. This is in contrast to New Zealand authors who have observed aggressive behaviour in *N. fucicola* (e.g. Francis, 1988; Paulin & Roberts, 1992). Differences between studies may relate to the population density or geographic location.

The absence of *N. fucicola* at night agrees with other labrid studies, where most fish are diurnal and inactive at night (e.g. Hobson *et al.*, 1981; Stephens & Zerba, 1981). Despite intensive searches only one *N. fucicola* was ever seen at night. This is similar to Choat (1962) who did not observe any *N. fucicola* during night dives. They may either move to deeper waters at night to 'sleep', bury themselves in sand or gravel, or hide in seaweed.

There is no doubt that *N. fucicola* is a territorial species but further research is required to resolve the rationale behind this behaviour. Additionally, it would be of interest to carry out tagging in New Zealand to investigate migration patterns and the home range of this species. Finally, little is known of the nocturnal habits of this species so intensive night dives could be conducted in order to further examine the nocturnal behaviour of *N. fucicola*.

CHAPTER SIX

CONCLUSIONS

6.1 CONCLUSIONS

This study investigated various aspects of the ecology of the banded wrasse, *Notolabrus fucicola*, a ubiquitous species around the Kaikoura Peninsula. Chapter Six summarises the findings of this thesis.

Confusion in the literature regarding the sexual system of *N. fucicola* is probably because this species displays characteristics of both protogynous and gonochoristic species. The present study found that *N. fucicola* is most likely a secondary gonochoristic species; 1) both males and females were represented throughout the size range which is indicative of species that do not change sex, 2) a residual ovarian lumen was found in an immature male, 3) the ratio of females to males was 1.6: 1 which is much lower than for protogynous species, and 4) histological staging revealed no evidence of transitional individuals or post-maturational sex change.

However, *N. fucicola* does not fit the typical pattern for gonochorism where males have little or no opportunity to change sex; 1) *N. fucicola* is not haremistic and does not appear to live at high population densities, 2) there is no evidence of nesting behaviour or parental care common in several gonochoristic species and 3) males and females have a similar growth rate. Additionally, 4) Dipper & Pullin (1979) proposed sex change was more likely to develop in large long lived species such as *N. fucicola* and 5) pair spawning in a lekking system observed by Jones (pers. com.) are the circumstances in which protogyny would be expected to evolve.

Several questions about the reproduction and behaviour of *N. fucicola* remain unresolved. Despite finding no transitional gonads, it is still possible that particular environmental or social conditions could induce sex change in at least a small proportion of fish as Jones (pers. com.) reported a small number of transitionals throughout the size range.

The spawning season of *N. fucicola* occurred from July until December. The onset of the spawning period appears to influence the condition and gut fullness of fish. These cycles are probably linked to changing water temperatures. Interestingly, the GSI of IP males peaked for only one month then immediately dropped back to pre-spawn levels. This suggests that small males spawn as often as possible early in the season, then once they are recognised and possibly excluded from mating by larger males, they divert energy into growth instead of reproduction.

It seems unlikely that territories are used for spawning because no courting or spawning behaviour was seen during the hundreds of dives during this project. Therefore territories are probably used primarily for feeding and the advent of spawning remains problematical. There is inferential evidence for group spawning. This is the mode used by *N. fucicola* in Australia. Furthermore, small males had similar GSI to larger ones, suggesting that they are not sneakers, as would be predicted in pair spawning. Additionally, the similarity of the male and female GSI indicates that *N. fucicola* are synchronous pelagic spawners.

N. fucicola are a monochromatic, monandric species, the opposite pattern to the closely related *Notolabrus celidotus*. The changeover from the initial phase to the terminal phase colouration occurs from approximately 200 to 300 mm. In most species, including *N. celidotus*, the changeover is associated with sex change. However, the significance of this colour change in *N. fucicola* is likely to be associated with a change in habitat or breeding status.

Both sexes grow to 100 mm in the first two to three years, after which they are sexually mature. The average age was 9 years but *N. fucicola* are slow growing and long-lived, reaching at least 25 years old. Because very large specimens were observed (but were not able to be aged), it is assumed that *N. fucicola* could live at least 35 years based on growth curves.

Few recruits of *N. fucicola* were seen in natural habitats, unlike *N. celidotus* which recruit abundantly into algal stands in shallow water. *N. fucicola* may

Few recruits of *N. fucicola* were seen in natural habitats, unlike *N. celidotus* which recruit abundantly into algal stands in shallow water. *N. fucicola* may have either patchy recruitment or recruit into deeper waters. Few *N. fucicola* were seen at night suggesting they move to deeper waters at night to 'sleep' or bury themselves in sand or gravel.

My study found similar results to other authors investigating the spatial and temporal distribution of reef fishes around New Zealand (e.g. Choat & Ayling, 1987). *N. fucicola* showed significant differences in numbers over time but no obvious patterns. *N. fucicola* numbers were evenly distributed across depths but different sizes were not. However, the usual pattern of increased size with depth was not observed. Instead the smallest fish were found at the intermediate depths (7 - 11 m).

N. fucicola are a generalist species consuming a wide range of prey. Almost all prey items in the guts of *N. fucicola* varied over time. For example, peaks occurred in amphipods and salps during summer. Variations in diet are probably influenced strongly by seasonal changes in prey populations. As is typical of most fish, there was an obvious shift in prey choice for *N. fucicola* with increasing size. Smaller fish, < 180 mm, fed mainly on soft-bodied animals, predominantly amphipods and isopods, while fish > 180 mm fed mostly on crabs, bivalves and gastropods. One interpretation of this dietary shift is a change in foraging habitat from macroalgae to rocky areas.

There are interesting differences between closely related *Notolabrus celidotus* and *N. fucicola*. These species are the most common labrids around New Zealand and inhabit the same areas. Additionally, wild hybrids have been recorded between these species (Ayling, 1982). However, *N. celidotus* is a protogynous hermaphrodite and dichromatic. What could be the mechanisms that could explain the observed differences between the two species? To help answer this question it would be of interest to examine other New Zealand labrids, such as the girdled wrasse, *N. cinctus*, and the scarlet wrasse, *Pseudolabrus miles*, to investigate and compare their reproductive biology and

social structure. As in *N. fucicola* and *N. celidotus*, *P. miles* are widely distributed throughout New Zealand while *N. cinctus* is a southern species. Most labrids in New Zealand are found only in the warmer waters of northern New Zealand. Knowledge of the life history and reproductive biology of other species may shed light on the general reproductive patterns of labrids in cold temperate waters.

The findings of this study will go towards clarifying some of the confusion that exists in the literature for the banded wrasse, *Notolabrus fucicola*, particularly the social and sexual system. If, in the future, a lucrative live fishery develops in New Zealand as currently occurs in Australia, it will be necessary to understand the ecology and biology of this species in order to avoid exploitation of the population.

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APPENDIX ONE

DIETARY ITEMS

Appendix 1. Dietary items, frequency of occurrence (FO) and mean volume (MV) of 450 *Notolabrus fucicola* sampled from December 1996 to February 1998 around the Kaikoura Peninsula. UI = Unidentified.

Prey category	Scientific name	Common name	FO(%)	MV(%)
MOLLUSCA				
Bivalvia	<i>Aulacomya maorianus</i>	Ribbed mussel	34.7	49
	<i>Modiolus aerolatus</i>	Hairy mussel	4.4	43
	<i>Mytilus edulis aoteana</i>	Little black mussel	2.6	35
Gastropoda	<i>Zeacumantus subcaratus</i>	Little turret shell	1.8	35
	<i>Trochus viridis</i>	Greentop shell	0.7	20
	<i>Antisolarium egenum</i>	Red shell	0.7	6
	<i>Maurea pellucida</i>		2.2	35
	<i>Cominella glandformis</i>	Mud whelk	2.4	3
	<i>Buccinulum lineum</i>		1.8	3
	<i>Soletellina nitida</i>	Golden sunset shell	0.2	1
	<i>Notoacmea pileopsis</i>		0.2	50
		UI snail shells	13.5	30
	<i>Cellana radians</i>	Radiate limpet	1.3	20
	<i>Cellana ornata</i>	Ornate limpet	3.5	6
		Unidentified limpet	1.1	8
	<i>Sypharochiton pelliserpentis</i>	Serpent chiton	2.2	30
		Unidentified chiton	0.2	16
	<i>Nototodarus</i> sp.	Squid	0.2	58
		UI shell fragments	26.3	18
ANNELIDA				
Polychaeta		Sedentary	3.8	30
		Errant	7.7	23
ARTHROPODA				
Crustacea				
Cirripedia	<i>Chthamilid</i>	Barnacle	0.2	15
Amphipoda	<i>Gammaridae</i>		22.5	20
	<i>Lysianassidae</i>		2.2	30
		UI amphipods	4.2	15
Isopoda	<i>Valvifera</i>		1.8	10
	<i>Asellota</i>		0.4	5
	<i>Anthuridae</i>		0.9	15
	<i>Flabellifera</i>		2.9	24

	Oniscoidea		4.9	19
		UI isopods	0.4	19
Decapoda	Plagusia chabrus	Red rock crab	5.7	35
	Notomithrax peronii		0.4	15
	Notomithrax ursus	Hairy seaweed crab	0.2	72
	Notomithrax minor		0.2	40
	Notomithrax sp.		0.2	19
	Trichoplatus huttoni	Huttons masking crab	0.9	76
	Eurynolamprus australis	Triangle crab	0.2	15
	Leptomithrax sp.	Spider crab	0.4	15
	Pilumnus novaezelandiae		0.2	80
	Hemigrapsus edwardsii	Purple rock crab	0.7	15
	Ovalipes catharus		0.2	20
	Halicarcinus varius		0.2	15
		Hermit crab	0.2	5
		Crab larvae	0.4	2
		UI crab fragments	18.8	25
	Jasus edwardsii	Crayfish	0.4	24
	Euphausid sp.		0.9	13
Echindermata				
Echinoidea	Evechinus chloroticus	Sea urchin	2.6	13
Urochordata				
Thaliacea		Salp	11.5	31
Ascidacea		Ascidean	1.8	15
Platyhelminthes				
Turbellaria	Chromoplana sp.		0.2	10
Vertebrata				
Teleostei		Fish	0.4	40
	Hippocampus sp.	Seahorse	0.2	30
		Bones	2.2	25
DETRITUS				
Seaweeds	Carpophyllum sp.	Brown seaweeds	10.4	6
	Carpococcus linearis			
	Plocamiaceae sp.	Red seaweeds	2.6	9
	Carpococcus linearis			
		Green seaweeds	4.2	5
Coralline algae	Corallina officinalis		16.6	3
Stones			12.6	3
Empty guts			1.8	0